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BIOENERGETICS OF THE BROWN LEMMING (*LEMMUS SIBIRICUS*)

A

DISSERTATION

Presented to the Faculty of the

University of Alaska in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

by

John W. Coady, M.S.

Fairbanks, Alaska

May 1975

BIOENERGETICS OF THE BROWN LEMMING (LEMMUS SIBIRICUS)

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ABSTRACT

Resting (M_{rest}), basal (M_b) and maximum (M_{max}) oxygen consumption were measured using an open circuit respirometer, and average daily metabolic rate (ADMR) was measured using a manometric respirometer on seasonally acclimatized and cold acclimated brown lemmings, Lemmus sibiricus. In addition, locomotor activity and rate and efficiency of assimilation of natural summer vegetation were determined. Resting metabolic rate and M_b of wild caught lemmings were significantly higher and M_{max} was significantly lower in 1968 than during corresponding seasons in 1969. Differences in subnivian temperatures during preceding winters probably accounted for annual changes in M_{rest} and M_{max}, although factors responsible for differences in M_b are unclear. Heat loss coefficients ranged from 20 to 50% below that predicted on the basis of body size. Basal metabolic rates ranged from 32 to 80% above that predicted by standard equations, although they are consistent with measurements from other Microtine species. Average daily metabolic rates of lemmings were significantly higher in -15°C acclimated animals than in spring, summer or fall acclimatized animals, apparently due to increased energy requirements for thermoregulation. Neither ADMR nor activity indices provided evidence for a circadian rhythm, although a pronounced short cycle with a period of four to five hours in both oxygen consumption and locomotor activity was clearly demonstrated. Food consumption was high and assimilation low, resulting in an efficiency of assimilation (31%) considerably below that measured for small mammals at more southern latitudes.

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INTRODUCTION

The distribution and ultimate survival of a species in an area is strongly influenced by the environment, and this influence is maximized in regions where climatic conditions reach their extremes. Arctic animals occupy the smallest of the world's climatic zones - a zone which is characterized not only by intense cold and near constant darkness during winter, but also by warmth and continuous light during summer. In short, the Arctic is a region of great annual fluctuation in both temperature and light regimes.

The terrestrial mammalian fauna of Arctic Alaska is limited to about 30 species (Rausch 1953). However, these range from the polar bear (Ursus maritimus) and moose (Alces alces), weighing over 600 kilograms, to the masked shrew (Sorex cinereus) weighing three grams. Over one-half of the mammalian species commonly found in the Arctic weigh less than 100 grams (Morrison 1964).

Perhaps the most distinctive small northern mammal is the brown lemming (Lemmus sibiricus) which occurs throughout arctic North America west of Hudson Bay. This species usually becomes more numerous from south to north and in Alaska is most abundant along the low, wet coastal tundra (Bee and Hall 1956). Four additional microtine rodents occur on the north slope of the Brooks Range, but near Point Barrow on the Arctic coast only the brown lemming and to a lesser extent the varying (collared) lemming (Dicrostonyx groenlandicus) are generally found.

The brown lemming is considered holarctic in distribution (Rausch

1961). Based primarily on morphological comparisons, Ognev (1947) stated that the Alaskan brown lemming was conspecific with the Siberian lemming, Lemmus obensis [now known as Lemmus sibiricus (Ellerman 1949)]. Although Siberian and Alaskan forms likely are conspecific, cytogenetic comparison is needed for conclusive proof (Rausch, pers. comm.). Pending completion of investigations, Lemmus sibiricus (Kerr) is provisionally used here rather than Lemmus trimucronatus alascensis (Merriam) to distinguish North American animals from the Barrow region.

Food chain relationships involving the brown lemming are limited in number, but those that do occur are unusually intense and frequently cyclic. Of primary importance in the tundra ecosystem of northern Alaska is the three to four year cycle of lemming abundance and associated vegetation-lemming-predator interactions. Plant consumption throughout the year is dominated by the lemming, and large fluctuations in herbage production and nutrient levels appear to be directly related to the intensity of lemming grazing (Pieper 1963). Carnivory is strongly associated with the lemming cycle, and numbers of mammalian and avian predators increase conspicuously during population highs (Pitelka et al. 1955, MacLean et al. 1974). Other more obscure components of the tundra ecosystem, such as arthropods and soil microorganisms may also be influenced by lemming abundance (MacLean and Pitelka 1971).

Ecology and bioenergetics of arctic birds and mammals have been discussed in several recent publications. Reviews by Morrison (1964), Irving (1964a, 1964b, 1972), and Dunbar (1968) and studies of willow ptarmigan, Lagopus lagopus (West 1968), snowy owls, Nyctea scandiaca

(Gessaman 1972), Arctic Fox, Alopex lagopus (Underwood 1971), caribou, Rangifer tarandus (McEwan 1970, McEwan and Whitehead 1970), moose (Gasaway and Coady 1974), and others have enhanced our understanding of bioenergetics of northern homeotherms. Methods used in bioenergetic studies have been described by Petrusewics (1967), Gessaman (1973) and Grodzinski and Klekowski (1975).

Except for estimates of assimilation rate and digestive efficiency (Batzli et al. 1975), energetic relationships of brown lemmings in North America have not been studied. However, energy requirements of both the varying lemming (Scholander et al. 1950, Hart and Heroux 1955) and the Norwegian lemming, Lemmus lemmus (Hissa 1968), have been examined. In view of both the dominant role of the brown lemming in the tundra ecosystem and the paucity of bioenergetic data concerning it, this study was designed to examine some bioenergetic relationships characteristic of this abundant and widely distributed arctic species.

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CHAPTER I

SEASONAL AND ANNUAL VARIATION IN TEMPERATURE-METABOLIC RATE RESPONSE OF THE BROWN LEMMING, *LEMMUS SIBIRICUS*

INTRODUCTION

The arctic is characterized by pronounced annual fluctuations in climatic conditions. Intense cold and constant darkness during winter are replaced by moderate temperatures and continuous light during summer. By virtue of its abundance and extensive distribution, the brown lemming, Lemmus sibiricus, is probably the most distinctive small mammal in Arctic North America. The species becomes more numerous from south to north and in Alaska is most abundant along the low, wet coastal tundra (Bee and Hall, 1956). Four additional microtine rodents occur on the north slope of the Brooks Range, but near Point Barrow on the Arctic coast only the brown lemming and to a lesser extent the varying (collared) lemming, Dicrostonyx groenlandicus, are generally found.

The ability of a species to survive climatic extremes of the arctic and subarctic has long interested phsyiologists, and since the early work of Scholander et al. (1950a, 1950b, 1950c), the study of temperature regulation in cold environments has proceeded intensively in rodents as well as in other homeotherms. Temperature regulation in small northern mammals was also studied by Irving and Krog (1954, 1955), Morrison and Tietz (1957) and Morrison et al. (1954), and more recently reviewed by Irving (1964a, 1964b, 1972), Hart (1957, 1963, 1971) and Morrison (1964).

Unfortunately, few bioenergetic relationships involving the brown lemming have been examined. Only fur insulation (Scholander et al. 1950a), cold tolerance (Folk, Ferguson and McKee 1969), assimilation rate and digestion of summer forage (Batzli et al. 1975, Coady, MS), and average

daily metabolic rate (Coady, MS) have been studied.

In addition, Andrews (1968, 1970), Andrews and Ryan (1971) and Andrews and Strohbehn (1971) have examined endocrine relationships and West and Coady (1974) have reported on tissue fatty acid composition of brown lemmings. However, heat production at various ambient temperatures has not been examined.

The purpose of this study was to determine the basal, resting and maximum metabolic rate of seasonally acclimatized and cold acclimated brown lemmings to provide a measure of their fundamental energy requirements dependent on season.

METHODS

This study is based on data obtained from approximately 200 brown lemmings captured within fifteen kilometers of the Naval Arctic Research Laboratory (71°18'N, 156°47'W). The Laboratory is located on the shore of the Arctic Ocean, approximately 10 km S.W. of Point Barrow, the northernmost point in Alaska (Fig. 1). Winters at Point Barrow are long, cold and dry; summers are short, cool and moist (Britton 1957). The average annual air temperature is -12.4°C (U.S. Weather Bureau). Temperatures above freezing are recorded on 110 days per year, while temperatures below freezing occur on 323 days per year. February is the coldest month with an average temperature of -28°C, while July is the warmest month with an average of 4°C.

Live animals were collected in spring 1968 and 1969 during and immediately after snow melt-off, in summer 1968 and 1969 during the warmest period of the year, and in fall 1968 preceding snow fall. Lemmings were also snap trapped during winter 1969. Live lemmings were hand caught with the aid of Eskimo children. Animals were flown to the Institute of Arctic Biology, Fairbanks, Alaska (64°50'N, 147°35'W) within one to four days after capture. Lemmings were individually caged in 15 X 30 X 15 cm high cages, provided with wood shavings, Purina Rabbit Chow, water or snow, and occasional lettuce, and maintained in an environmental control room under a temperature and light regime representing the season at Barrow during which each group of animals was captured (Table 1). Animals were held in the environmental control room for three to four

Figure 1. Map of Alaska, showing Point Barrow, area in which brown lemmings were obtained.

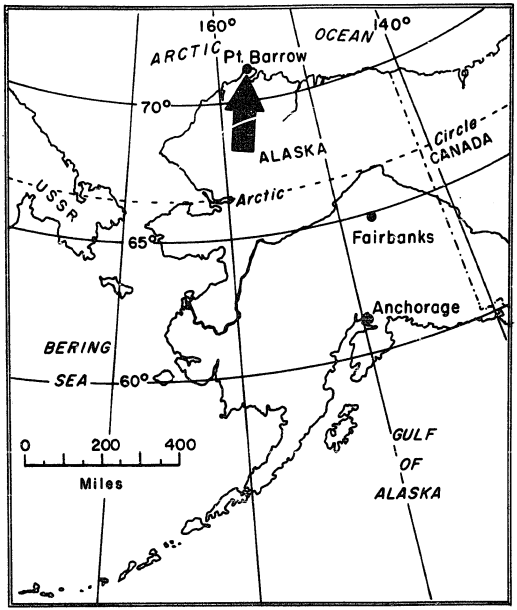


TABLE 1. Seasonal temperature and light regime under which captured animals were maintained prior to and during testing.

Season	Lab temp °C	Lab light (L:D) hrs
Spring	5	24:0
Summer	10	24:0
Fall	5	12:12
Winter	-15	3:21

days prior to and during the course of testing.

Live animals were not obtained in fall 1969 or in winter during any year. Therefore lemmings captured during summer 1969 were first acclimated to 5°C and 12 hours light (L):12 hours dark (D) during fall 1969 for one month and tested, and then to -15°C and 3L:21D during winter for two months and again tested (Table 1). Five °C acclimated animals were caged as described above while -15°C acclimated lemmings were provided with a larger 15 X 90 X 15 cm high cage filled with snow and hay, plus chow.

Only lemmings weighing between 30 and 100 grams were tested to exclude very young and very old or obese animals.

Resting (M_{rest}), basal (M_b) and maximum oxygen consumption (M_{max}) were measured with an eight channel open flow respirometer designed and built at the Institute of Arctic Biology (Morrison and West 1975). A single large vacuum pump ventilated room air at a given rate through the metabolism chamber connected to each respirometer channel. Gas was sampled from individual channels by shunting the flow through solenoid valves with a second pump to an infrared carbon dioxide analyzer (Beckman IR-215), a paramagnetic oxygen analyzer (Beckman F-3) and a wet test flow meter. Gas analyzer outputs and flow rates were recorded on a dual pen strip chart recorder (although only oxygen consumption data are reported here), and metabolism chamber temperatures and sample gas temperatures were recorded on a 20-point thermocouple recorder.

Metabolism chambers were constructed from three pound coffee cans, 15 cm in diameter, cut to a height of 10 cm (volume 1.8 liters). The

lip of the can was firmly inserted into a groove milled in a three mm thick plexiglass top and held in place with two rubber bands. The plexiglass was fitted with a hole for a thermocouple lead and copper intake and outlet tubes. The tubes contained several small ports to enhance mixing and uniform sampling of gas. Slight negative pressure within the metabolism chamber assured that any gas flow between the can and the lid would be inward. Flow rates were adjusted between 0.7 and 1.0 liters per minute to maintain an oxygen concentration in metabolism chambers of 19.5% or greater. Flow volumes were corrected to standard temperature and pressure, and oxygen comsumption vaues were corrected according to the appropriate formula in Depocas and Hart (1957).

Animals were tested at temperatures between 30 and -78°C ($\pm$ 0.1°C) in a reach-in Missmers Environmental Control Unit. Light was present during all tests.

Resting metabolic rate was measured on non-fasted animals at various ambient temperatures between 10 and -50°C. Six animals were individually placed in metabolism chambers along with rabbit chow, shavings, and water or snow. The chambers were ventilated with the large respirometer vacuum pump, and the animals cooled in the control unit to the appropriate seasonal acclimation temperature for a 12 to 15 hour adjustment period prior to testing. During tests 45 minutes to one hour were allowed after each temperature change for equilibration before oxygen consumption was recorded. Rectal temperatures were occasionally measured after testing to assure maintenance of homeothermy in the cold.

Basal metabolic rate, defined as the lowest average oxygen consumption

recorded at a particular thermal neutral zone temperature, was measured on postabsorptive lemmings at various temperatures between 10 and 30°C. Test procedure was similar to that described above except that no food was provided and only four hours were allowed prior to testing for adjustment and fasting. Respiratory quotients calculated for some individuals indicated that the animals were in a postabsorptive condition.

A non-fluctuating oxygen consumption record for a minimum of three minutes was required before M_{rest} or M_b data were accepted as the required minimum values. Due to frequent activity of animals, however, minimum values were usually obtained from only a portion of the individuals measured at each temperature.

Maximum oxygen consumption was measured by maintaining an animal in a metabolism chamber with shavings and rabbit chow at -75 to -78°C. Oxygen consumption was monitored until it began to decline, thereby suggesting a loss of body temperature. The animal was then removed and its rectal temperature measured to confirm hypothermia. Maximum oxygen consumption, measured at the greatest deflection of the recording pen, was calculated only for animals with a post-test rectal temperature of 36°C or below. This body temperature appears to be the lower limit from which many small mammals can spontaneously rewarm in the cold (Morrison, unpublished).

Fur length was measured on the flank of either live or dead lemmings using a calibrated probe. Most animals were adults although a few of the smaller individuals were subadults.

Linear regression lines fitted to individual values of M_{rest} were

compared by analysis of covariance. Paired sample means were compared using Student's t test, while more than two means were compared using Duncan's New Multiple Range Test incorporating Kramer's modification for unequal sample sizes. No statistically significant difference between sexes was observed, and therefore all data reported are for both males and non-pregnant, non-lactating females. Unless otherwise stated, 0.05 was the probability level at which the null hypothesis was rejected.

RESULTS

1. Resting Oxygen Consumption

Resting oxygen consumption was measured on lemmings wild caught during five seasons between spring 1968 and summer 1969 and acclimated to 5°C and 12L:12D hours during fall 1969, and to -15°C and 3L:21D hours during winter 1970 (Fig. 2, 3 and 4, Table 2). A least squares linear regression extrapolated to y = 0 (y = metabolic rate) has been fitted to the data for each season. At zero oxygen consumption these standard regression lines extrapolate to ambient temperatures between 32 and 46°C. At environmental temperatures below thermoneutrality, M_{rest} of lemmings is probably proportional to the temperature difference between the body and environment, $M = C(T_b - T_a)$, where M = metablic rate, C = thermal conductance, and T_b and T_a = body and ambient temperature, respectively (see discussion). Therefore, it may be more accurate to force linear regression lines through a body temperature of 38°C at y = 0. Slopes and/or elevations of forced regression lines from consecutive seasons during 1968 decrease significantly, while those from consecutive seasons in 1969-70 are not significantly different (Table 3). Both slopes and elevations of forced regression lines of acclimatized lemmings from spring, summer and fall 1968 are significantly greater than those of acclimatized or acclimated lemmings from corresponding seasons in 1969 (Table 3).

Figure 2. Average resting (M_{rest}) and basal (M_b) oxygen consumption, standard deviation (triangles), and range (bars) of brown lemmings wild caught during spring, summer and fall 1968. Numbers indicate sample size. Where standard deviation and/or range are omitted, they are too small to be shown. Slopes of dashed and solid lines indicate the best regression fit and the best regression fit through the point y=0, x=38, respectively, to the M_{rest} data. M_b is shown as the lowest average value at a particular temperature.

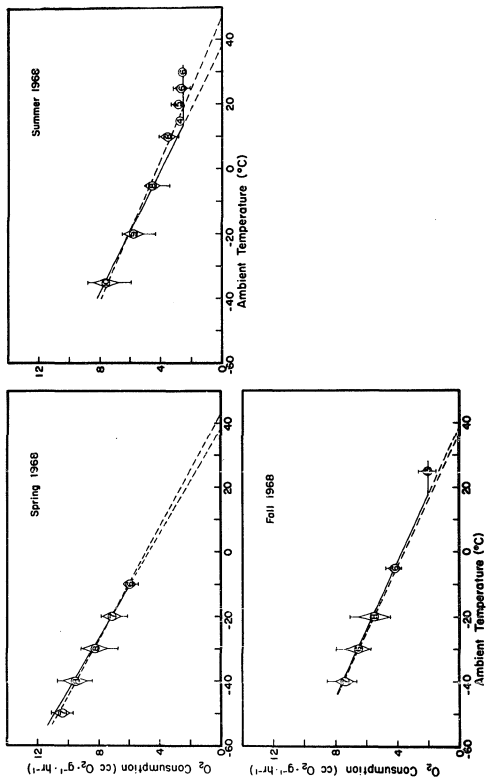


Figure 3. Average resting (M_{rest}) and basal (M_b) oxygen consumption, standard deviation (triangles) and range (bars) of brown lemmings wild caught during spring and summer 1969, and cold acclimated during fall 1969 and winter 1970. Numbers indicate sample size. Where standard deviation and/or range are omitted, they are too small to be shown. Slopes of dashed and solid lines indicate the best regression fit and the best regression fit through the point y=0, x=38, respectively, to the M_{rest} data. M_b is shown as the lowest average value at a particular temperature.

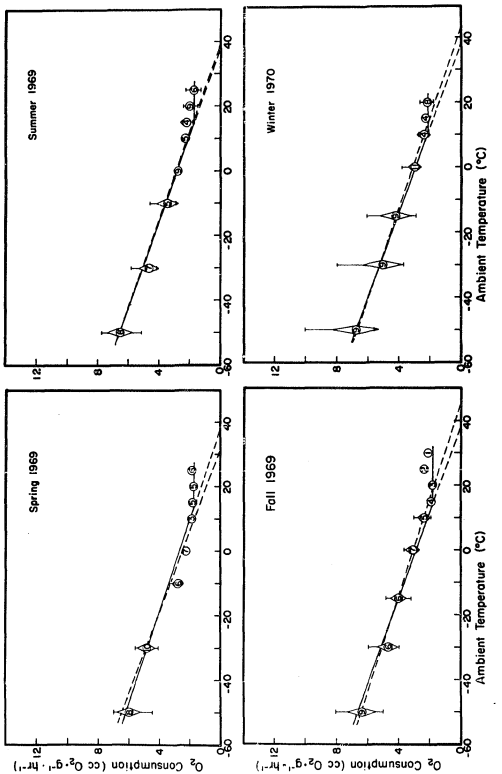


Figure 4. Summary of resting and basal oxygen consumption of brown lemmings during seven seasons. Slopes of lines indicate the best regression fit through the point y=0, x=38 to the resting oxygen consumption data.

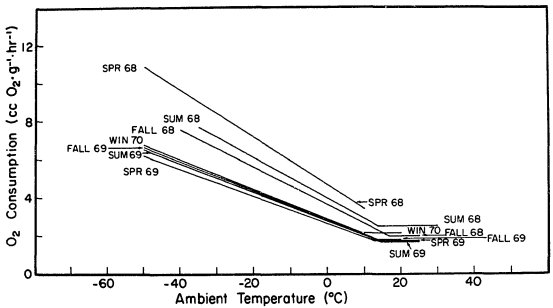


TABLE 2. Resting oxygen consumption of brown lemmings wild caught between spring 1968 and summer 1969, and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	n	Animal wt (g) ± 1 S.D.	Equation of standard least squares fit[1] and (forced fit)[2] regression lines	Correlation coefficient(r)
Spring 1968	11	44.4 ± 6.7	$y = 4.93 - 0.114x$[1]	-0.93
			$(y = 4.66 - 0.123x)$[2]	-0.93
Summer 1968	12	38.3 ± 4.6	$y = 4.28 - 0.091x$	-0.93
			$(y = 4.01 - 0.105x)$	-0.91
Fall 1968	9	44.8 ± 9.6	$y = 3.64 - 0.098x$	-0.88
			$(y = 3.67 - 0.097x)$	-0.88
Spring 1969	13	53.1 ± 7.9	$y = 2.52 - 0.079x$	-0.95
			$(y = 2.71 - 0.071x)$	-0.91
Summer 1969	9	55.7 ± 11.8	$y = 2.89 - 0.074x$	-0.94
			$(y = 2.86 - 0.075x)$	-0.94
Fall 1969	9	60.2 ± 14.3	$y = 3.10 - 0.068x$	-0.91
			$(y = 2.88 - 0.076x)$	-0.88
Winter 1970	15	57.0 ± 10.4	$y = 3.16 - 0.072x$	-0.81
			$(y = 2.98 - 0.078x)$	-0.80

[1]Least squares linear regression.
$y = cc O_2 \cdot g^{-1} \cdot hr^{-1}$
$x = $ temp °C

[2]Regression forced through 38°C ambient temperature at zero metabolism.
$y = cc O_2 \cdot g^{-1} \cdot hr^{-1}$
$x = $ temp °C

TABLE 3. Seasonal difference in resting oxygen consumption of brown lemmings determined by analysis of covariance of standard regression lines.

Comparison		F, (d.f.)	P = 0.05	Level of probability
SPR 68 - SPR 69	Slope	15.83 (1, 68)	SIG	P<0.005
	Elev	422.63	SIG	P<0.005
SUM 68 - SUM 69	Slope	4.62 (1, 65)	SIG	P<0.05
	Elev	118.38	SIG	P<0.005
FALL 68 - FALL 69	Slope	7.26 (1, 59)	SIG	P<0.01
	Elev	48.71	SIG	P<0.005
SPR 68 - SUM 68	Slope	5.10 (1, 67)	SIG	P<0.05
	Elev	45.61	SIG	P<0.005
SUM 68 - FALL 68	Slope	0.32 (1, 61)	NOT SIG	P>0.25
	Elev	8.00	SIG	P<0.01
SPR 69 - SUM 69	Slope	0.53 (1, 66)	NOT SIG	P>0.25
	Elev	0.75	NOT SIG	P>0.25
SUM 69 - FALL 69	Slope	0.87 (1, 63)	NOT SIG	P>0.25
	Elev	0.37	NOT SIG	P>0.25
FALL 69 - WIN 70	Slope	0.17 (1, 67)	NOT SIG	P>0.25
	Elev	0.50	NOT SIG	P>0.25

2. Basal Metabolic Rate

Basal metabolic rate was measured above 10°C in six groups of brown lemmings (Fig. 2, 3 and 4, Table 4). Basal metabolic rate decreased significantly between summer and fall 1968 to low values during all seasons in 1969, and increased significantly again in animals acclimated to -15°C during winter 1970. No significant difference was found in M_b of animals from spring, summer and fall 1969, and between fall 1968 and winter 1970.

Lower critical temperatures based on standard regression lines ranged from 19°C during summer 1968 to 10°C during spring 1969 (Fig. 2, 3 and 4), and averaged 15.4°C. Lower critical temperatures based on forced regression lines ranged from 17°C during fall 1968 to 11°C during winter 1970 (Fig. 2 and 3), and averaged 13.4°C. Upper critical temperatures were not determined. Ambient temperatures of 26 to 30°C either failed to produce a measureable increase in oxygen consumption (summer 1968) or resulted in the death of lemmings during tests (spring, summer, fall 1969, winter 1970). Gasping respiration and loss of muscular control was characteristic of these animals before death. Hart and Heroux (1955) attributed a similar phenomenon among varying lemmings exposed to 30°C or higher to heat stroke.

3. Maximum Oxygen Consumption

Maximum oxygen consumption measured at -75°C in seven groups of lemmings progressively increased during 1968 to high values in 1969-70 (Fig. 5, Table 5). No significant difference in M_{max} was found in animals

TABLE 4. Basal oxygen consumption (M_b) of brown lemmings wild caught between summer 1968 and summer 1969, and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	n	Animal wt (g) ± 1 S.D.	M_b ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$) ± 1 S.D.	Significance Range[1]
Summer 1968	6	37.8 ± 2.9	2.47 ± .24	
Fall 1968	14	44.6 ± 11.3	1.98 ± .27	
Winter 1970	10	55.6 ± 9.8	2.10 ± .28	
Spring 1969	11	51.8 ± 11.5	1.71 ± .18	
Summer 1969	9	51.0 ± 10.6	1.69 ± .28	
Fall 1969	5	56.1 ± 11.9	1.75 ± .08	

[1]Solid bar indicates no significant difference between sample means as measured by Duncan's new multiple range test, incorporating Kramer's modification for unequal sample size.

Figure 5. Average maximum oxygen consumption, standard deviation (triangles) and range (verticle lines) of brown lemmings during seven seasons. Numbers indicate sample size.

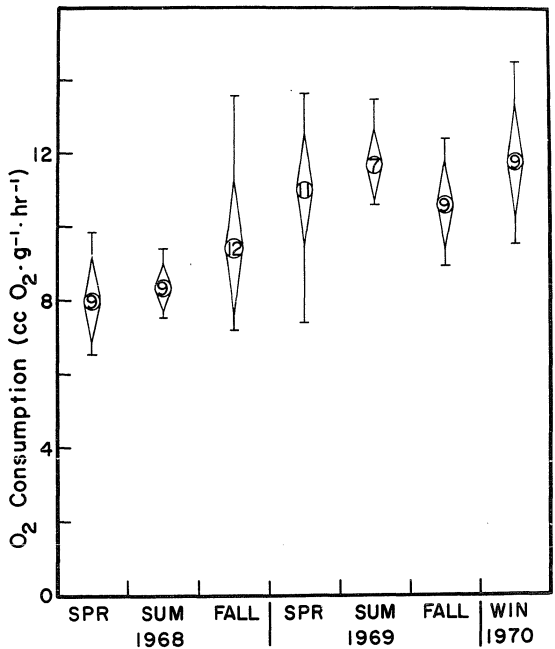


TABLE 5. Maximum oxygen consumption (M_{max}) of brown lemmings wild caught between spring 1968 and summer 1969, and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	n	Animal wt (g) ± 1 S.D.	M_{max} ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$ ± 1 S.D.	Significance Range[1]
Spring 1968	9	53.1 ± 5.2	7.98 ± 1.14	
Summer 1968	9	39.1 ± 4.3	8.36 ± 0.63	
Fall 1968	12	51.7 ± 13.7	9.42 ± 1.78	
Fall 1969	9	68.5 ± 18.9	10.60 ± 1.18	
Spring 1969	11	59.9 ± 19.2	10.99 ± 1.48	
Summer 1969	7	62.6 ± 15.9	11.67 ± 0.96	
Winter 1970	9	63.5 ± 11.9	11.79 ± 1.57	

[1]Solid bar indicates no significant difference between sample means as measured by Duncan's new multiple range test, incorporating Kramer's modification for unequal sample size.

acclimatized during spring and summer 1969 and cold acclimated during fall 1969 and winter 1970. Values from spring and summer 1968 were significantly lower than those from corresponding seasons in 1969.

4. Fur Length

All fur length measurements were obtained from wild caught lemmings, except during fall 1969 and winter 1970 when 5°C and -15°C acclimated animals were used, respectively. Length of fur from the flank in eight groups of lemmings increased progressively from an average of 15.0 mm during spring 1968 to an average of 19.9 mm during spring 1969 or greater during other seasons between fall 1968 and winter 1970 (Fig. 6, Table 6). No significant difference in fur length of lemmings was measured between fall 1968 and winter 1970. However, lengths from spring and summer 1968 were significantly shorter than those from corresponding seasons during 1969.

Figure 6. Average fur length, standard deviation (triangles) and range (verticle lines) of brown lemmings during eight seasons. Numbers indicate sample size.

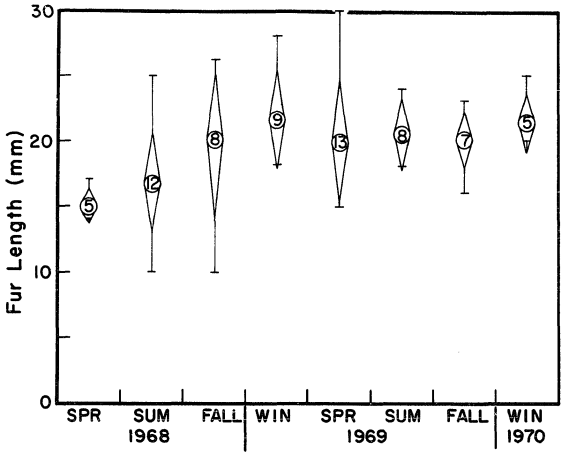


TABLE 6. Flank fur length of brown lemmings captured between spring 1968 and summer 1969, and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	n	Animal wt (g) ± 1 S.D.	Fur length (mm) ± 1 S.D.	Significance Range[1]
Spring 1968	5	48.2 ± 14.3	15.0 ± 1.2	
Summer 1968	10	53.3 ± 27.6	16.7 ± 3.6	
Fall 1968	6	45.2 ± 10.6	20.1 ± 6.1	
Winter 1969	9	49.9 ± 6.2	21.7 ± 3.7	
Spring 1969	12	73.8 ± 10.9	19.9 ± 4.6	
Summer 1969	8	62.1 ± 8.6	20.5 ± 2.7	
Fall 1969	7	58.0 ± 7.6	20.1 ± 2.2	
Winter 1970	5	66.3 ± 22.1	21.4 ± 2.2	

[1]Solid bar indicates no significant difference between sample means as measured by Duncan's new multiple range test, incorporating Kramer's modification for unequal sample size.

DISCUSSION

1. Resting Oxygen Consumption

Principles of thermoregulation in birds and mammals have been discussed at length by numerous authors (Scholander et al. 1950a, 1950b, 1950c; Hart 1957, 1963; King and Farner 1961; Kleiber 1961; West 1962; Gelineo 1964; Folk 1966; Bartholomew 1968; Whittow 1971; and Precht et al. 1973).

Thermal equilibrium between a homeotherm and its environment, resulting in maintainance of body temperature, depends upon a balance between mechanisms of heat loss and heat gain. At moderate temperatures most homeotherms exhibit a zone of thermoneutrality, where heat production is minimal and virtually independent of ambient temperature. Heat loss at temperatures within the thermal neutral zone is controlled by physical mechanisms, such as piloerection, posture, rate and pattern of blood circulation, and evaporation of water. At temperatures below thermoneutrality increased heat loss must be compensated for by increased heat production. The temperature of which physical mechanisms of heat conservation are maximum and where a further decrease in ambient temperature requires an increase in metabolism is termed the lower critical temperature.

The rate of heat loss by an organism below the lower critical temperature is proportional to the temperature difference between the body and the environment. A convenient physical description of this relationship, originally applied to homeotherms by Scholander et al.

(1950b) and more recently examined by McNab (1970) and Kleiber (1972) is found in Newton's Law of Cooling: $\frac{dH}{dt} = C(T_b - T_a)$, where C is a cooling constant, usually referred to as thermal conductance, and T_b and T_a are body and ambient temperature, respectively. For a body with a given heat capacity the rate of heat flow is proportional to the rate of heat loss. Therefore, rate of heat loss from a homeotherm = $C(T_b - T_a)$, and if body temperature is closely regulated, T_b is constant, and metabolic rate (M) = $C(T_b - T_a)$. Newton's Law does not apply to homeotherms at thermal neutral zone temperatures, since M is constant and C is variable. However, at temperatures below the lower critical temperature C is minimum, and M is proportional to the difference in temperature between the body and the environment.

If animals conform to Newton's Law, M should extrapolate to zero when $T_a = T_b$. In this study, rectal temperatures which were occasionally measured immediately after M_{rest} and M_b tests consistently indicated a T_b of 38 to 39°C. Since excitement caused by handing tends to elevate body temperature (Morrison and Ryser 1959), normal T_b may have been slightly lower than those measured. The relationship of $T_a = T_b$ when $M \simeq 0$ was found among lemmings measured during fall 1968 and summer 1969 (Fig. 2 and 3). During all other seasons except for spring 1969, T_a was greater than T_b when M = 0 (Fig. 2 and 3).

Assuming T_b remains relatively constant, departures from Newton's Law may be due to activity or to changes in C (Hart 1971). Spontaneous activity elevates oxygen consumption. During tests between 10 and -50°C, lemmings were frequently more active at warmer than at colder temperatures.

This would tend to elevate oxygen consumption above resting values at warm temperatures, resulting in extrapolation of T_a above T_b at M = 0. In addition, metabolic thermoregulation may begin before C reaches a minimum value. If M begins to increase while C is still decreasing at temperatures near the lower critical temperature, the result would be a curvilinear correlation between M and T_a, and extrapolation of T_a to a higher temperature than T_b when M = 0. However, this does not invalidate the application of Newton's Law to thermoregulation of homeotherms, since the Law is simply a mathematical approximation of the rate of temperature loss, and does not consider biological features. McNab (1970) has stressed the mathematical convenience of using Newton's Law to describe heat flux in homeotherms at ambient temperatures well below thermoneutrality.

In spite of the small deviations from the general relationship $M = C(T_b - T_a)$ found during some seasons, brown lemmings do comply with Newton's Law (Fig. 2 and 3). Extrapolation of the temperature-metabolic rate curve from four seasons to a T_a greater than T_b when M = 0 is probably due to activity and possibly to changes in C at temperatures near the lower critical temperature. I have no explanation for the extrapolation of T_a below T_b at M = 0 found during spring 1969. The linear regression of M on T_a forced through T_b minimizes deviations from Newton's Law at moderate temperatures, and facilitates comparison of M_{rest} between different groups of lemmings. West (1972a, 1972b) has forced the linear regression of M on T_a through T_b to describe M_{rest} of rock ptarmigan (Lagopus mutus) and common redpolls (Acanthis flammea) in Alaska.

Most homeotherms conform to Newton's Law (Scholander et al. 1950b, Morrison and Ryser 1951, Irving and Krog 1955, McNab and Morrison 1963, Hayward 1965, Wunder 1970, Coulombe 1970). However, some exceptions attributed to changes in conductance have been noted for small mammals (Hart and Heroux 1955, Beck and Anthony 1971) and birds (West 1962).

The factor C in Newton's Law is thermal conductance, and is a measure of the rate at which heat is lost. In a regression of M on T_a below thermoneutrality the slope of the line represents thermal conductance, and has the units of $cc O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1}$. Average values of C decreased during consecutive seasons in 1968 to low values in 1969-70 (Table 7). Thermal conductance was 78, 43 and 20% greater during spring, summer and fall 1968, respectively, than during corresponding seasons in 1969. Thermal conductance was not significantly different among lemmings from four seasons in 1969-70.

Total conductance of mammals is determined by body size (surface area) and conductance of the fur (McNab and Morrison 1963). Body size is related to surface area by the relationship $S = 10W^{.67}$, where S = surface area in cm^2, and W = body weight in g (Kleiber 1961). Thus, if conductance of the fur is unchanged, an increase in body size and therefore surface area of lemmings will result in an increase in thermal conductance. Conductance during three seasons in 1968 when body weights averaged less than 50 g were slightly greater than during four seasons in 1969-70 when body weights averaged greater than 50 g (Table 7). Therefore, smaller body size of lemmings during 1968 did not contribute to higher conductance values during that period vs. 1969-70.

TABLE 7. Average thermal conductance (C) of brown lemmings wild caught between spring 1968 and summer 1969 and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

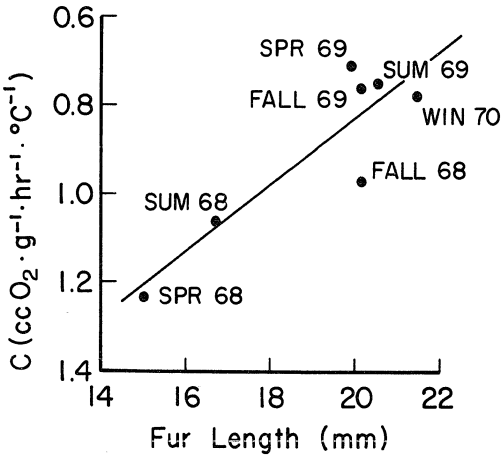
Season	Animal wt (g) ± 1 S.D.	Temp range (°C)	No. of measurements	C ($cc O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1}$) ± 1 S.D.
Spring 1968	44.4 ± 6.7	-10 to -51	36	0.123 ± 0.009
Summer 1968	38.3 ± 4.6	+11 to -35	35	0.109 ± 0.016
Fall 1968	44.8 ± 9.6	-4 to -43	27	0.095 ± 0.010
Spring 1969	53.1 ± 7.9	+10 to -47	34	0.069 ± 0.009
Summer 1969	55.7 ± 11.8	+10 to -48	34	0.076 ± 0.009
Fall 1969	60.2 ± 14.3	+10 to -49	33	0.079 ± 0.012
Winter 1970	57.0 ± 10.4	+3 to -50	38	0.080 ± 0.016

Scholander at al. (1950a), Hart (1956) and Morrison and Tietz (1957) have demonstrated that insulation is proportional to fur length. Since insulation is the reciprocal of conductance (Scholander et al. 1950b), the contribution of the pelt to the total conductance of the animal can be estimated by plotting length of fur of lemmings during each season against total conductance (Fig. 7). As fur length increased, total conductance decreased during consecutive seasons in 1968. During all seasons in 1969-70, fur length remained relatively long and total conductance remained relatively low. While both body surface and insulation of the pelt determine total conductance of animals, the pelt appears to exert a greater influence in brown lemmings. This is in agreement with Hart's (1971) conclusions that for most mammals, total conductance is determined primarily by fur insulation, and not by surface-weight relationships. Thus, differences in slopes of M_{rest} of brown lemmings in this study may be primarily related to differences in insulation of the fur.

Only one other study has reported a difference in metabolic rate of a homeotherm during the same season in successive years. Hart et al. (1965) found a 10-15% difference in oxygen consumption both within and below thermoneutrality of varying hares (Lepus americanus) measured during two consecutive summers. No explanation for the difference was given.

Herreid and Kessel (1967) have predicted thermal conductance based on conductance values taken from the literature of 24 mammals: $\log C = 0.691 - 0.505 \log W$, where W = body weight in g. This equation is similar to $\log C = 0.681 - 0.501 \log W$ developed from measurements of Wisconsin

Figure 7. Average thermal conductance related to fur length of brown lemmings.



mammals by Morrison and Ryser (1951). Thermal conductance of brown lemmings in this study ranged from 20% in spring 1968 to 50% in spring 1969 lower than predicted from the above equations. Therefore, total insulation of brown lemmings appears to be considerably greater than that of most other small mammals. Other values for thermal conductance of brown lemmings are not available. However, Scholander et al. (1950b) found C = 0.074 $cc O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1}$ and Hart and Heroux (1955) found C = 0.110 $cc O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1}$ for varying lemmings collected during winter at Barrow, Alaska, and during summer at Fort Churchill, Manitoba, respectively. Conductance values for varying lemmings during winter were similar to those obtained for brown lemmings in this study during all seasons in 1969-70.

The lack of seasonal changes during 1969 in oxygen consumption of both wild caught and cold acclimated brown lemmings differs from that of many other small mammals. Wild caught Dicrostonyx groenlandicus (Scholander et al. 1950b, Hart and Heroux 1955), Clethrionomys glareolus (Pearson 1962), and numerous other species show a lower heat production at a given temperature in winter than in summer. However, Hart (1957) found no difference in metabolic rate below thermoneutrality in Peromyscus measured during winter and summer. The similarity in metabolic response to cold temperatures in spring and summer 1969 acclimatized brown lemmings (Fig. 3 and 4) probably reflect the lack of pronounced seasonal changes in over all body insulation or conductance. The similarity in lower critical temperatures during the two seasons also suggests that insulative differences are insignificant. Lack of seasonal changes in insulation

are probably due to the short summer season and the relatively cold ground level temperatures which persist throughout the year (Fig. 7). Kelley and Weaver (1969) found that average ground level temperatures near Barrow ranged from a low of -21°C in March to a high of only 5°C during July.

2. Basal Metabolic Rate

Basal metabolic rate is a measure of energy requirements for minimum physiological function. Ideally, test conditions for measuring M_b include postabsorptive state, complete inactivity, and "comfortable" microclimate (Benedict 1938). In practice, these conditions may be difficult if not impossible to attain, particularly with wild species. The extent to which psychological, physiological and physical stresses on an animal can be reduced vary greatly among individuals and species. Consequently, the circumstances appropriate for measuring M_b will vary with the species, and the accuracy of measurement will largely depend upon the extent to which stresses can be minimized. While strict use of the term M_b may frequently not be applicable, it is a useful comparative concept, providing the technical difficulties of its measurement are realized.

It is well known that M_b of mammals increases as an exponential function of body weight. The Brody-Proctor formula (Brody 1945) specifies $M = 70W^{.73}$, while Kleiber (1961) suggests that $M = 70W^{.75}$, where M is in Kcal/day, and W = body weight in Kg, is a better approximation. In this study the lowest metabolic rate for each individual during each season

plotted against body weight produced a metabolic rate-weight relationship of $M = 91W^{.70}$ ($r = 0.75$). Hayward (1965) calculated an average regression coefficient of 0.69 for several subspecies of Peromyscus, while Wiegert (1961) found a regression coefficient of 0.52 for fed and 0.64 for fasting Microtus pennsylvanicus. Hart (1971) reviewed other studies in which regression coefficients ranged from 0.20 to 0.94.

While the regression coefficient describing the M_b-body weight relationship for brown lemmings is similar to that predicted by Brody (1945) or Kleiber (1961), the elevation of the relationship is somewhat higher than that given by standard curves. Basal metabolic rates of brown lemmings in this study ranged from 32% in summer 1969 to 80% in summer 1968 higher than predicted by Kleiber (1961) (Table 8).

From data available at the time, Scholander et al. (1950c) concluded that M_b is phylogenetically not adaptive to climate, although they acknowledged that metabolic rates may be found to be adaptive in animals living under arctic and tropic extremes. Subsequent studies have indeed suggested that phylogenetic patterns may exist among certain groups of rodents. From his own studies of Microtus montanus and from a review of the literature, Packard (1968) suggested that species of the sub family Microtinae have M_b values higher than predicted from standard metabolic rate-body weight curves. He speculated that since Microtinae are of boreal origin (Hooper 1949) their high M_b may be related to problems of temperature regulation. Since most microtines live at ambient temperatures below thermoneutrality, a high M_b per se does not result in an increased energy expenditure, while a greater heat production

TABLE 8. Measured and predicted basal metabolic rate (M_b) of brown lemmings wild caught between summer 1968 and summer 1969 and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	Avg wt (g)[1]	Measured M_b ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	Predicted M_b ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	% difference measured/predicted
Summer 1968	37.8	2.47	1.38	+80
Fall 1968	44.6	1.98	1.32	+50
Spring 1969	51.8	1.71	1.27	+35
Summer 1969	51.0	1.69	1.28	+32
Fall 1969	56.1	1.75	1.25	+40
Winter 1970	55.6	2.10	1.25	+68

[1]From Table 4.

[2]$M_b = 70W^{.75}$, 4.8 cal = 1 $cc O_2$

does result in enhanced survival in the cold (Scholander et al. 1950c, Hart 1957). Beck and Anthony (1971) reviewed metabolic patterns for several species of Microtus and Cleithrionomys, and found that M_b ranged from 40 to 112% higher than that predicted from the Brody-Proctor formula (Brody 1945). Basal metabolic rates of brown lemmings measured in this study fall well within this range of values.

Several workers have also noted that rodents from hot climates have a reduced M_b relative to predicted values. McNab and Morrison (1963) found lower M_b values among subspecies of Peromyscus inhabiting deserts than among non-desert subspecies. Hart (1971) summarized several studies and noted that numerous groups of rodents inhabiting deserts and arid regions have M_b values which average about 10% below the standard curve. Recently, Wang et al. (1973) reported M_b values for the Arctic hare (Lepus arcticus) of 17-38% below that predicted on the basis of body size.

Factors responsible for differences in M_b of lemmings between seasons and between years are difficult to explain. Body size is generally the most important factor regulating M_b (Scholander et al. 1950c). However, when M_b during each season is expressed as a function of $W^{.70}$ calculated for lemmings in this study, differences in M_b between easons are only slightly reduced (Table 9), and significant differences between seasons as measured by Duncan's New Multiple Range Test remain unchanged. Therefore, weight differences do not appear to be responsible for observed differences in M_b.

Hayward (1965) suggested that differences in M_b independent of

TABLE 9. Basal metabolic rate (M_b) and metabolic body weight specific M_b of brown lemmings wild caught between summer 1968 and summer 1969, and acclimated to 5°C during fall 1969 and to -15°C during winter 1970.

Season	Avg wt (g)	$W_B^{.75}$	M_b ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)[1]	M_b ($cc O_2 \cdot g^{-.30} \cdot hr^{-1}$)[1]
Summer 1968	37.8	15.3	2.47	6.10
Fall 1968	44.6	17.3	1.98	5.10
Spring 1969	51.8	19.3	1.71	4.59
Summer 1969	51.0	19.1	1.69	4.51
Fall 1969	56.1	20.5	1.75	4.79
Winter 1970	55.6	20.4	2.10	5.72

[1]Solid bar indicates no significant difference between sample means as measured by Duncan's new multiple range test, incorporating Kramer's modification for unequal sample size.

weight may be due to differences in body composition, particularly fat. Since fat contributes relatively little to M_b, a fat animal would have a lower M_b per gram of body weight than would a lean animal. Consistent with Hayward's (1965) hypothesis, highest M_b (Table 4) and leanest body mass (Coady, unpubl.) were found in lemmings during summer 1968. However, low M_b and lean body mass were found during spring 1969. The fattest lemmings were found during fall 1968, a season of intermediate M_b values. High M_b during winter 1970 could have been due to the influence of lean body mass on metabolic rate. However, it was more likely due to an increased heat production at thermal neutral zone temperatures after cold acclimation (Hart 1957, 1971). While elevated M_b values following cold acclimation is not a universal feature of all species, it has been demonstrated in a number of laboratory animals. Therefore, while lean body mass may have been responsible for high M_b values of lemmings during some seasons, no consistent relationship between body fat and M_b was found.

Differences in M_b may also be due to temperment (Hayward 1965) or to diet (Morrison et al. 1959) of animals. While not obvious, lemmings may have been more excitable, resulting in a higher M_b, during summer and fall 1968 than during 1969. Further, diet of wild animals change seasonally, and therefore changes in the gut in response to specific foods probably occur. However, the influence of diet in affecting the results of this study are unknown.

The similarity of M_b between spring 1969 and summer 1969 wild caught lemmings suggests that seasonal changes in metabolic rate at thermoneutrality can be small or non-existent (Table 4). Basal metabolic

rates of most small wild caught mammals, including the varying lemming (Scholander et al. 1950b, Hart and Heroux 1955), the red-backed vole, Clethrionomys glareolus (Pearson 1962), and several microtine species reviewed by Hart (1971) are lowest in winter and highest in summer. However, Heroux, Depocas and Hart (1959) found no significant difference among winter and summer acclimatized white rats. The similarity in both M_{rest} and M_b between spring and summer acclimatized brown lemmings may be due to the relatively cool summer temperatures and short summer season at Barrow compared with that to which small mammals at more southern latitudes are exposed. Cool ambient temperatures near the ground throughout most of the year (Fig. 8) result in cold acclimatization of lemmings during all seasons.

The best estimate of M_{rest} and M_b can be obtained by pooling groups which are not significantly different. Resting metabolic rates and M_b from spring, summer and fall 1969 are not significantly different (Tables 3 and 4), and therefore the data have been grouped (Fig. 9). The temperature-metabolic rate line extrapolates to 38°C, and has the equation $y = 2.83 - 0.074X$. Basal metabolic rate is 1.78 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$, and the critical temperature is 14°C. Until the higher metabolic rates found during spring, summer and fall 1968 are more fully understood, and until additional studies have been conducted to determine the oxygen consumption of winter acclimatized animals, the data grouped above are assumed to represent the best approximation of M_b and M_{rest} of brown lemmings during all seasons at Barrow, Alaska.

Figure 8. Average ground level temperature on beach ridge near Barrow, Alaska, 1965-66. Snow cover from October through May virtually eliminates diurnal fluctuations in ground level temperature during this period (from Kelley and Weaver 1969).

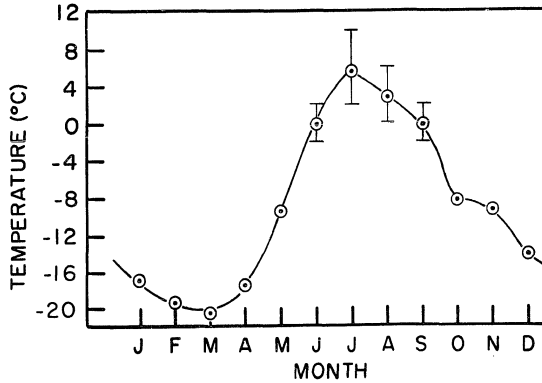
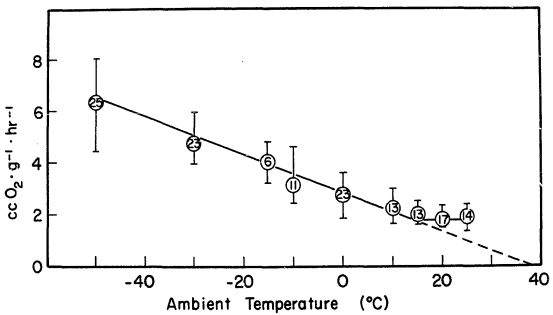


Figure 9. Average and range of resting and basal oxygen consumption of brown lemmings wild caught at Barrow, Alaska during spring and summer 1969 and acclimated during fall 1969. Numbers indicate sample size. Standard deviations are too small to show. Slope of resting metabolic rate is computed by the method of least squares, and basal oxygen consumption is the lowest average value at a particular temperature.



3. Maximum Oxygen Consumption

Maximum metabolic rate is the highest measurable rate of oxygen consumption that can be sustained for several minutes (Hart 1957). Maximum metabolic rate is generally elicited by very low temperature and/or intensive activity, although recently a high conductance atmosphere of helium and oxygen and moderately cold temperature has been used by Rosenmann and Morrison (1974). Under conditions eliciting M_{max} heat loss soon exceeds heat production, and animals lower their oxygen consumption as they become hypothermic. Therefore, it is important to attain the values of M_{max} as soon as possible after beginning the experiment (Jansky 1965).

Maximum metabolic rate in cold adapted animals is proportional to the total oxidative capacity of all tissues. Cytochrome oxidase is the last link in the chain of oxidative enzymes, and is responsible for at least 90% of all cellular oxidations in most species (Commoner 1940). Therefore, the total oxidative capacity of the animal will probably not be greater than the activity of this enzyme. Cytochrome oxidase activity has been found to correspond to M_{max} in several mammals, including the rat (Jansky 1963), and several species of voles (Heimer, unpubl.)

Chemical thermal regulation during cold exposure may result from shivering and/or nonshivering thermogenesis. Shivering thermogenesis results from energy released by muscular actions or tremors which do not perform mechanical work. Shivering thermogenesis is a major source of heat production in warm acclimated mammals (Jansky 1965), and is apparently the only source of heat production (other than specific

dynamic action) in adult birds (Hart 1962, West 1962, 1965).

Nonshivering thermogenesis has recently been reviewed by Jansky (1973). It is a mechanism of heat production resulting primarily from the calorigenic action of noradrenaline released from sympathetic nerve endings, and having its greatest thermogenic effect in skeletal muscle and brown adipose tissue. Nonshivering thermogenesis is an important source of heat production in newborn animals, hibernators, cold-exposed mammals and some neonatal birds (Wekstein and Zolman 1968).

The increased capability of nonshirvering thermogenesis during cold exposure is an important aspect of cold acclimation and acclimatization. Jansky (1965, 1973) and Hart (1971) have reviewed studies which demonstrate that the metabolic response to noradrenaline in several species increases by a magnitude of up to three times M_b with decreasing acclimation or acclimitization temperature. Thus, while both shivering and nonshivering thermogenesis are important for heat production at very low temperatures (Jansky and Hart 1963), nonshivering thermogenesis is probably the most important source of heat production determining metabolic capability in the cold (Jansky 1969).

Maximum metabolic rate of brown lemmings measured during this study increased during 1968 from 7.98 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in spring 1968 to 11.69 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in summer 1969 and 11.79 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in winter 1970 (Fig. 5, Table 5). Maximum values ranged from 3.38 to 6.91 times measured M_b during summer 1968 and summer 1969, respectively (Table 10). Maximum values ranged from 6.10 to 9.74 times M_b calculated from Kleiber's (1961) equation during summer 1968 and winter 1970, respectively. Hart (1971)

TABLE 10. Ratio of maximum oxygen consumption (M_{max}) to measured and calculated basal oxygen consumption (M_b), and metabolic expansivity ($M_{max} - M_b$) of brown lemmings.

Season	Meas M_b[1] ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	Calc M_b[2] ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	M_{max}[3] ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	$\frac{M_{max}}{Meas\ M_b}$	$\frac{M_{max}}{Calc\ M_b}$	M_{max} - Meas M_b ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)
Spring 1968	.--	1.27	7.98	--	6.28	--
Summer 1968	2.47	1.37	8.36	3.38	6.10	5.89
Fall 1968	1.98	1.27	9.42	4.76	7.42	7.44
Spring 1969	1.71	1.23	10.99	6.43	8.34	9.28
Summer 1969	1.69	1.21	11.67	6.91	9.64	9.98
Fall 1969	1.75	1.19	10.60	6.06	8.91	8.85
Winter 1970	2.10	1.21	11.79	5.61	9.74	9.69

[1] From Table 4.

[2] $M_b = 70W^{\cdot 75}$, 4.8 cal = 1 $cc O_2$.

[3] From Table 5.

reviewed the literature and reported that M_{max} averaged about 7 times M_b ($M_b = 70W^{.70}$), while Jansky (1965) concluded that maximum values equal about 10 times M_b ($M_b = 70W^{.75}$). Values for brown lemmings obtained during 1969-70 fell well within the 7 to 10 times M_b range predicted by Hart (1971) and Jansky (1965), while those obtained during spring and summer 1968 were somewhat lower. Therefore, during all seasons in 1969-70 lemmings had a greater capacity for heat production than during 1968.

It has been established that M_{max} is strongly influenced by past thermal history. Cold acclimated white rats are capable of higher oxygen consumption than are warm acclimated animals (Krog et al. 1955, Depocas, Hart and Heroux 1963, Heroux et al. 1959). Wild rats (Ratus norvegicus) caught and tested during winter were also capable of higher M_{max} than were animals captured and tested during summer (Hart and Heroux 1963). Hart (1957) reviewed additional studies which indicate that survival time in extreme cold is greater among cold exposed animals than among warm exposed animals. More recently, Folk, Ferguson and McKee (1969) reported an increase in cold tolerance from summer to winter by a factor of 1.7 to 51.0 for several species of wild caught rodents. Rosenmann et al. (1975) found an increase in M_{max} of 16.6 to 26.4 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ between summer and winter acclimatized Clethrionomys rutilus (wt = 15-16 g). This amounted to an increase of 9.3 to 14.5 times the theoretical M_b. Similarly, Feist and Rosenmann (1975) found a 25% increase in M_{max} between summer and winter acclimatized snowshoe hares, Lepus americanus.

Increases in M_{max} of brown lemmings from 1968 to 1969-70 may have been due to differences in cold exposure during the two preceding winters. Although insulation provided by snow in Arctic Alaska is not as great as that provided by snow at more southern latitudes (Benson 1969, Kelley and Weaver 1969), it does, nevertheless, result in a subnivian microclimate warmer than that above the snow cover (Coady, unpubl.). The degree of insulation is determined in part by the depth of snow. Snow depths during the 1967-68 winter were approximately 30% greater than during the 1968-69 winter (Fig. 10). The greater snow depths and probably warmer subnivian temperatures during the 1967-68 winter may have been responsible for a lower maximum metabolic capability of lemmings during the following seasons. In addition, temperatures were colder and precipitation was greater during summer 1969 than during summer 1968 (Fig. 11). This, too, may have resulted in greater cold expsoure, and consequently a greater metabolic capability of wild caught lemmings during 1969 than during 1968. Laboratory acclimation temperatures of 5°C during fall 1969 and -15°C during winter 1970 apparently maintained a high metabolic capability in lemmings during those seasons. Lack of distinct seasonal differences in M_{max} of brown lemmings may be due to consistently cool ambient temperatures to which lemmings are exposed during all seasons, as compared to seasonal temperatures at more southern latitudes.

Maximum metabolic rates of brown lemmings do not appear to be directly proportional to the degree of previous cold exposure. Maximum values do not necessarily follow seasonal temperature rhythms (Hart 1971), and in fact, Rosenmann et al. (1975) reported that the seasonal increase in M_{max}

Figure 10. Snow depth on the ground during winters 1967-68 and 1968-69 at Barrow, Alaska (from U.S. Department of Commerce).

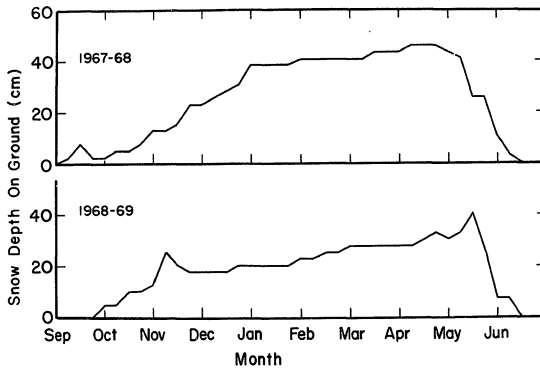
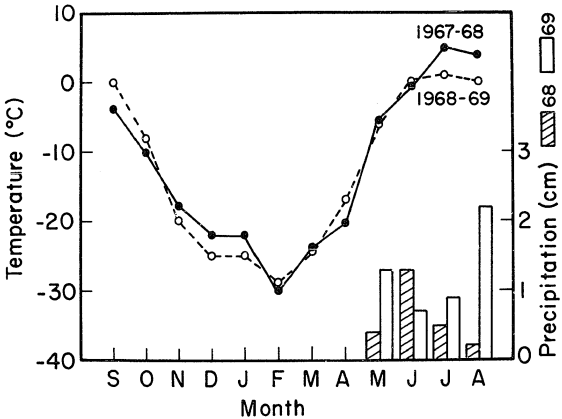


Figure 11. Average temperature between September 1967 and August 1969 and total precipitation during summers 1968 and 1969 at Barrow, Alaska (from U.S. Weather Bureau).



of Clethrionomys anticipates winter cold by one month. Therefore, the influence of environmental factors (eg., photoperiod) other than temperature must be considered. Insulation and body size are apparently not responsible for differences in M_{max} (Jansky 1965) or cold tolerance (Folk, Ferguson and McKee 1969) of small mammals.

4. Fur Length

As noted above, numerous authors have reported a correlation between fur length and insulation of the pelt, and recently Brown and Lasiewski (1972) have used hair length of long tailed weasels (Mustela frenata) to indicate the relative insulation of fur. Scholander et al. (1950a) demonstrated a positive relationship between fur length and body size of small mammals weighing less than 4 kg. Among small Arctic mammals, body size apparently determines the length of fur which will maximize insulation without restricting mobility. Scholander et al. (1950a) found no correlation between body size and fur length among animals weighing greater than 4 kg. All large mammals, regardless of size, had approximately the same insulation per unit of surface area.

Average fur length of brown lemmings during different seasons ranged from 15.0 mm to 21.7 mm (Table 6). These values agree closely with those reported for lemmings in other studies. Scholander et al. (1950a) found fur lengths of 15-22 mm for brown lemmings collected at Barrow during winter. Bee and Hall (1956) reported fur lengths of about 17 mm during September and about 21 mm during June for brown lemmings in Northern Alaska. Scholander et al. (1950a) measured fur length of 19-21

mm for varying lemmings during winter at Barrow, and Hart (1956) reported similar values for the species in the Northwest Territories.

Factors responsible for an increase in hair length of lemmings between 1968 and 1969 are unclear. Animals were collected in spring and summer during the two years at similar times, i.e. in spring during and immediately following snow melt, and in summer during the warmest time of year. Therefore, animals should have been at comparable stages of molt during corresponding seasons. In addition, only fur length of lemmings weighing greater than 40 g were measured, thereby avoiding juveniles in the sample.

Both hormones and nutrition may have a profound affect on hair growth. Several gonadal and adrenal steroid hormones, such as oestrogens, androgens and glucocorticoids may inhibit hair growth in certain species, including rodents (Houssay et al. 1965). Andrews (1968) and Andrews and Strohbehn (1970) demonstrated seasonal and yearly differences in endocrine functions of brown lemmings at Barrow, Alaska. However, there is no clear relationship between the results reported by these authors and hair lengths reported in this study.

Flesch (1954) and Lorencz (1954) have discussed the influence of nutritional deficiencies, including amino acids, proteins, vitamins, fatty acids and minerals on hair growth. Pieper (1963) demonstrated seasonal and yearly fluctuations in mineral composition of tundra plants at Barrow, Alaska associated with the intensity of lemming grazing. For example, concentrations of phosphorus, potassium and nitrogen in vegetation tended to decrease throughout the growing season, and to be minimum during

years following a lemming high. However, the relationship between lemming density and apparent intensity of grazing and hair length found in this study is obscure.

As noted above, Scholander et al. (1950a) reported a correlation between body size and fur length among Arctic mammals weighing less than 4 kg. However, differences in body size were not related to seasonal and yearly differences in hair length of lemmings. Apparently within the small range of body weights encountered in this study (Table 6), weight related differences in fur length were masked by other factors.

The most likely explanation for seasonal and yearly differences in hair growth found in this study is temperature. Differences in subnivian temperatures during 1967-68 winters due to differences in snow depths (Fig. 10) may have contributed to increased hair length between 1968 and 1969. The relatively warm and dry summer in 1968 compared to 1969 (Fig. 11) may also have contributed to differential hair growth between the two years. The probable influence of amibent temperature on pelage of captive brown lemmings was also apparent. Lemmings captured during 1968 and 1969 near Barrow and maintained in an Institute of Arctic Biology colony at 20°C had shorter and less dense fur than animals used in this study which were maintained at 10 to -15°C. An increase in pelage density of Clethrionomys during winter vs. summer was observed by Selander (1972).

SUMMARY

In spite of several notable contributions during the past 20 years, the study of energetics in arctic ecosystems is still in its infancy. This work established certain metabolic parameters of an important arctic herbivore, the brown lemming, which permits a better understanding of the species' successful adaptation to arctic conditions.

While certain aspects of M_{rest}, M_b and M_{max} of brown lemmings were similar to those reported for rodents at lower latitudes, several important differences exist. Although small deviations from expected relationships occur, brown lemmings conformed to Newton's Law of cooling, and M_{rest} extrapolated to approximately body temperature during most seasons. When M_{rest} of lemmings from different seasons which were not significantly different were grouped, the temperature-metabolic rate line extrapolated to body temperature. The regression coefficient of M_b on body weight of 0.70 for lemmings was similar to that predicted by standard equations (Brody 1945, Kleiber 1961). Further, the similarity of M_b in winter and summer acclimatized lemmings, and the increase of M_b in cold acclimated animals supports most earlier observations on small mammals.

Conductance of brown lemmings ranged from 20 to 50% below that predicted by Herreid and Kessel (1967), apparently because of greater fur insulation than expected for mammals of that body size. The similarity of M_{rest} in spring and summer acclimatized lemmings differs from observations in many other small mammals, and may be due to consistently cool and relatively small seasonal changes in temperatures

near the ground compared to that at lower latitudes. However, higher conductance of lemmings during 1968 than during the same seasons in 1969 were probably due to increased fur insulation resulting from colder subnivian temperatures during the winter of 1968-69 *vs.* 1967-68.

Basal metabolic rates ranged from 32 to 80% above that predicted by Kleiber (1961). However, M_b above standard rates are consistent with measurements on other Microtine rodents, and tend to support the hypothesis that M_b may be phylogenetically adaptive to climate in some groups of mammals. Factors responsible for higher M_b of lemmings during 1968 than during 1969 are unclear.

Maximum metabolic capability is influenced largely by previous cold exposure. Unlike most observations in which winter acclimatized or cold acclimated rodents have higher M_{max} than summer acclimatized or warm acclimated animals, no difference in M_{max} of lemmings during 3 seasons in 1969 or with cold acclimation was observed. The similarity in M_{max} of lemmings captured during spring and summer 1969 and animals acclimated to 5°C and to -15°C may also be due to relatively uniform and cool temperatures to which animals were exposed. Lower M_{max} of lemmings from three seasons 1968 *vs.* the same season in 1969 may be due to colder subnivian temperatures during winter 1968-69 than during the previous winter.

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CHAPTER II

SEASONAL METABOLISM AND LOCOMOTOR ACTIVITY OF THE BROWN LEMMING, *LEMMUS SIBIRICUS*

INTRODUCTION

The brown lemming (Lemmus sibiricus) occurs throughout most of Arctic North America west of Hudson Bay, and locally extends into alpine and boreal habitats of subarctic regions (Hall and Kelson 1959). However, the species usually becomes more numerous from south to north, and in Alaska is most abundant along the low, wet coastal tundra (Bee and Hall 1956). Seasonal extremes in temperature and light contribute to a low diversity of arctic mammals (Dunbar 1968). While more mobile species such as caribou (Rangifer tarandus) and moose (Alces alces) may occur along the Arctic coast during summer, relatively few mammals are permanent residents of this harsh environment. Of the microtine rodents, only the brown lemming and to a lesser extent the varying (collared) lemming (Dicrostonyx groenlandicus) are generally found.

The existence of brown lemmings in the Arctic implies adequate adaptation to their environment. Their small, compact body with short ears and tail appears to be well insulated. Active throughout the year, animals minimize climatic extremes of winter by remaining under the snow, where activities are carried out in an extensive subnivian environment of runways, spaces and nests. In summer, animals utilize burrows and runways dug in the soil and under mats of decaying vegetation for shelter and protection.

The role of the brown lemming in the Arctic ecosystem has been examined in several recent studies. The three to four year cycle of lemming abundance has been documented at Barrow since 1946 (Rausch 1950,

Thompson 1955a, 1955c; Pitelka 1957a, 1957b, 1973). Thompson (1951, 1955a, 1955b, 1955c), Pitelka (1957a, 1957b) and Batzli et al. (1975) have discussed habitat preference, and Brooks and Banks (1971) have examined home range and activity patterns of free ranging lemmings. Food habits and the impact of lemming grazing on the vegetation has been studied by Pieper (1963) and Batzli et al. (1975), while the role of predation in lemming cycles has been discussed by MacLean et al. (1974). However, the bioenergetics of brown lemmings has received little attention until recently. Batzli et al. (1975) have examined assimilation rate and efficiency of digestion of lemmings during summer, and Coady (MS) has studied basal, resting and maximum oxygen consumption of wild caught lemmings during several seasons. Recently, Collier et al. (1975) have reviewed and developed a mathematical model of energetic relationships of brown lemmings, utilizing in part data reported in this paper.

Consistent with IBP Tundra Biome objectives, this study was designed to contribute to understanding the role of brown lemmings in the tundra ecosystem. In view of the paucity of bioenergetic data regarding the brown lemming, some physiological and behavioral characteristics associated with the successful adaptation of the species to its arctic environment have been examined. Energy requirements of lemmings under natural conditions were estimated by measuring seasonal and diurnal changes in oxygen consumption and locomotor activity, and by measuring rate and efficiency of assimilation of natural summer vegetation.

METHODS

1. Study Area

This study is based on data obtained from brown lemmings captured within fifteen kilometers of the Naval Arctic Research Laboratory (71°18'N, 156°47'W). The Laboratory is located on the shore of the Arctic Ocean, approximately 10 km S.W. of Point Barrow, the northernmost point in Alaska (Fig. 1). The arctic coastal plain, upon which Barrow is located, is an emergent portion of the continental shelf extending into the Chukchi and Beaufort Seas. Dominant surface features of the tundra near Barrow consist of low relief, shallow elliptical lakes and drained lake basins, and tundra polygons (Hussey and Michelson 1966). Poor surface drainage results in numerous shallow lakes and marshes covering 50 to 75% of the land. Most marsh areas occur in former lake basins which are subject to flooding during spring melt, and frequently remain saturated throughout the summer.

Winters at Barrow are long, cold and dry; summers are short, cool and moist (Britton 1957, AINA 1974). The average annual air temperature is -12.4°C (U.S. Weather Bureau). Temperatures above freezing are recorded on 110 days per year, while temperatures below freezing occur on 323 days per year. February is the coldest month with an average temperature of -28°C, while July is the warmest month with an average of 4°C (Fig. 2). Mean annual precipitation is 116 mm. However, Black (1954) indicated that actual precipitation may be two to four times greater due to gauging inefficiencies caused by high winds. Approximately half of the precipitation

Figure 1. Map showing location of Point Barrow, the region where brown lemmings were captured.

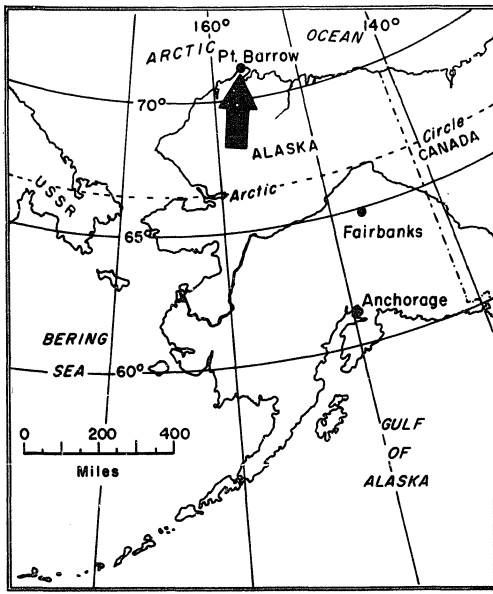
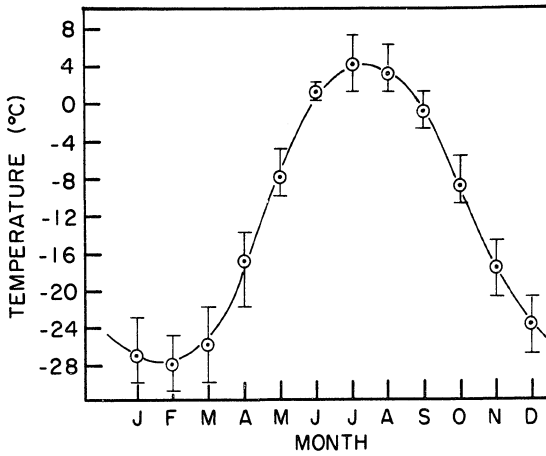


Figure 2. Fifty year average maximum, average mean and average minimum air temperature at Barrow, Alaska (from U.S. Weather Bureau).



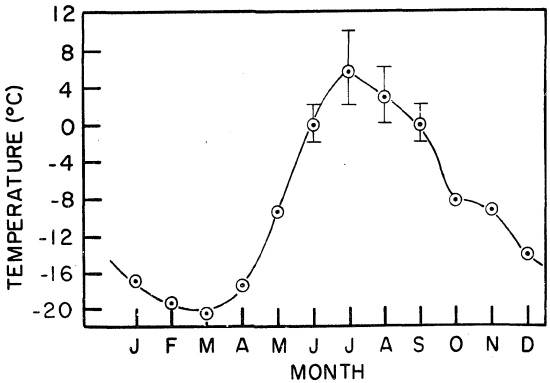
falls as snow, producing a yearly average of 67 cm. Heavy fog, cloud cover and high humidity persist during much of the summer. In spite of low rain fall, precipitation equals or slightly exceeds total evapotranspiration during the summer (Mather and Thornthwaite 1956).

Temperature variations at the tundra surface near Barrow have been studied by Kelley and Weaver (1969) (Fig. 3). Although measurements were made on an old beach ridge, Kelley (pers. comm.) predicted that surface temperatures in less elevated areas would be similar to those on the beach ridge. From October through May, the eight coldest months of the year, and in July and August, the two warmest months of the year, average surface temperature was -14.5 and 4.1°C, respectively. Both in June and in September, months of thawing and refreezing, the average surface temperature was 0°C.

Ground level temperatures recorded in 1953-1954 near Barrow at Special Hole No. 36 by the United States Geological Survey (Marshall, pers. comm.) averaged approximately -13, 7 and 4°C, respectively, for the same periods described above.

Both plant and animal species diversity in the Barrow area is low. Plants consist primarily of herbaceous perennials and low shrubs (Wiggins and Thomas 1962, Britton 1957, Hultén 1968). Of the 106 species of vascular plants listed by Hultén (1961) as occurring near Barrow, Pieper (1963) indicated that 75 of them belong to only seven families. The brown lemming and to a lesser extent the varying or collared lemming are the only important herbivores. Caribou and moose rarely pass through the area and therefore are not significant herbivores. Mammalian lemming

Figure 3. Average ground level temperature on beach ridge near Barrow, Alaska, 1965-66. Snow cover from October through May virtually eliminates diurnal fluctuations in ground level temperature during this period (from Kelley and Weaver 1969).



predators, listed in likely order of importance, are the least weasel, Mustela nivalis, the arctic fox, Alopex lagopus, the short tailed weasel or ermine, Mustela erminea, and the red fox, Vulpes fulva. During the summer a large number of shorebirds, ducks, geese, jaegers, gulls, owls and some passerines migrate into the area. Major avian lemming predators are the pomarine jaeger, Stercorarius pomarinus, the snowy owl, Nyctea scandiaca, and the short-eared owl, Asio flammeus (Pitelka et al. 1955, Maher 1970). The snowy owl is the only bird which occasionally winters near Barrow.

2. Study Techniques

Lemmings used in this study were collected in spring 1969 during and immediately after snow melt-off, in summer 1968 and 1969 during the warmest period of the year, and in fall 1968 preceding snow fall. All lemmings were hand caught with the aid of Eskimo children. Live animals were flown to the Institute of Arctic Biology, Fairbanks, Alaska (65°50'N, 147°35'W) within one to four days after capture. Lemmings were individually caged in 15 X 30 X 15 cm cages, provided with wood shavings, Purina Rabbit Chow, water or snow, and occasional lettuce, and maintained in an environmental control room under a temperature and light regime representing the season at Barrow during which each group of animals was captured (Table 1). Animals were held in the environmental control room for three to four days prior to and during the course of testing.

Live animals were not obtained in fall 1969 or in winter during any year. Therefore lemmings captured during summer 1969 were first

TABLE 1. Seasonal temperature and light regime under which captured lemmings were maintained prior to and during testing.

Season	Temp °C	Photoperiod (L:D)
Spring	5	24:0
Summer	10	24:0
Fall	5	12:12
Winter	-15	3:21

acclimated to 5°C and 12 hours light (12):12 hours dark (D) during fall for one month and then to -15°C and 3L:21D during winter for two months before testing (Table 1). Fall animals were caged as described above while winter acclimated individuals were provided with a larger 15 X 90 X 15 cm high cage filled with snow and hay, plus chow.

Only lemmings weighing between 30 and 100 grams were tested to exclude very young and very old or obese animals.

Average daily metabolic rate (ADMR) was measured under temperature and light regimes representing the season of animal capture (spring, summer, fall) or acclimation conditions (winter) using an automatic manometric respirometer (Morrison 1951). The system provides a record of oxygen consumption by injecting and measuring the time required for an animal to consume a fixed quantity of oxygen from a metabolism chamber.

Individuals were held in a 15 X 35 X 13 cm high, 3 mm mesh stainless steel cage with chow, lettuce, and nest can, and enclosed in a 20 liter stainless steel chamber with plexiglass top. Baralyme served as a carbon dioxide absorbant, and a saturated solution of calcium chloride maintained the relative humidity near 30 to 40% at temperatures between 5 and 10°C. Metabolism chamber size and design was similar to that recommended by the International Biological Program for studying small mammal bioenergetics (Morrison and Grodzinski 1968). A thermostatically controlled water or ethylene glycol bath and an overhead timer light were used to cool and light two chambers during each test. After a four hour equilibration period oxygen consumption was monitored for 40 to 45 hours.

Animals were weighed to the nearest 0.1 gram before and after all

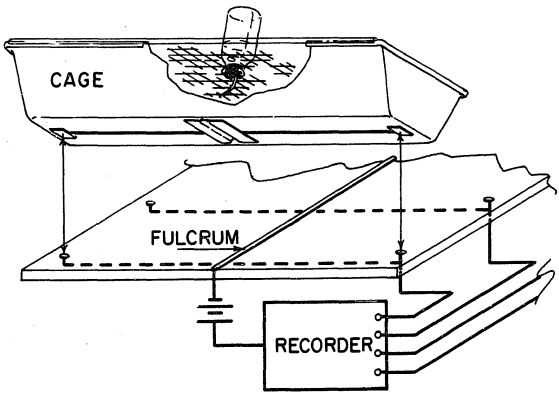
oxygen consumption tests and average body weights were used in calculations. All oxygen consumption values were corrected to standard temperature and pressure.

Rate of assimilation and assimilation efficiency of tundra vegetation was measured at 10°C and 24L:0D hours in 21 X 28 X 21 cm high stainless steel metabolism cages equipped with water bottle and nesting can. A stainless steel funnel below the cage directed feces, urine and some particles of vegetation into a collecting beaker.

Fresh stands of herbage, especially the grass Dupontia fischeri and the sedges Eriophorum spp. were clipped at ground level near Barrow during summer, mixed to form a homogenous sample, and frozen in heavy plastic bags. Animals captured during summer were fed vegetation in metabolism cages for three days prior to testing to flush the alimentary tract of chow and to readjust to a natural diet. During each test, which lasted six days, parcels of vegetation were wrapped into tight bales with wire to reduce scattering, weighed to the nearest 0.01 gram, and fed ad libitum to each animal. After three and six days, respectively, animals were weighed, and all excrement and unused food removed and separated. Any egesta remaining on the cage floor and funnel sides were washed into the collecting beaker with distilled water. Dried samples of vegetation samples and feces plus urine were ground through a 60 mesh screen in a Wiley Mill and the caloric value determined with a Parr adiabatic oxygen bomb calorimeter.

Locomotor activity was measured in four 15 X 90 X 15 cm high cages containing chow and shavings at each end and a water bottle in the middle (Fig. 4). A 10 X 15 cm grooved copper plate glued to the middle of a

Figure 4. Diagram of one activity cage and recorder. The cage is balanced on the fulcrum, and as an animal moves from one side of the fulcrum to the other the electrical circuit is momentarily broken and the activity recorder triggered.



cage bottom rested on a 5 mm diameter copper rod fulcrum. A 3 X 6 cm copper plate glued to each end of the cage bottom was electrically wired to the center plate. The four copper rod fulcrums, electrically wired together, and eight copper plates opposing those on each end of the four cage bottoms were mounted on a plywood board. The rod and plates on the board were wired through a 12 volt power supply and four channels of an Esterline Angus event recorder. When an animal moved across the fulcrum and tipped the cage, the circuit was momentarily broken and the recorder triggered. An animal was placed in each activity cage and after a four hour adjustment period, activity was recorded for approximately three days. An activity index of 0 to 30 was calculated by the number of two minute intervals per hour in which activity occurred.

An IBM 360/40 computer program normalized ADMR to equal time intervals and calculated a mean, range and standard deviation of oxygen consumption for each animal. An IBM 1620 computer and California Computer Products (CALCOMP) plotter graphed oxygen consumption for each individual. No significant difference between sexes was found, and therefore all data reported are for both males and non-pregnant, non-lactating females. Unless otherwise stated, 0.05 was the probability level at which the null hypothesis was rejected in all tests.

RESULTS

Oxygen Consumption

The Average Daily Metabolic Rate was highest in lemmings acclimated to -15°C during winter and lowest in animals captured during spring, although only winter values differed significantly from those in other seasons (Fig. 5, Table 2). Oxygen consumption ranged from 5.90 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in winter to 3.79 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in spring, with intermediate values of 4.46 and 4.24 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in summer and fall, respectively. No circadian rhythm in oxygen consumption was detected in either constant light (spring and summer) or in changing photoperiod (fall and winter), as shown by individual records of daily oxygen consumption of representative animals (Fig. 6-9). However, a short term cycle of oxygen consumption was evident in all animals tested during each season. The average period of the short cycles during each season was not significantly different, and ranged between 4 and 5 hours (Fig. 10). The average amplitude of the cycles was significantly greater during winter than during other seasons (Fig. 11). The relatively large standard deviation in ADMR during winter also reflects the greater variability in oxygen consumption during that season (Table 2).

Food Consumption

Rate of food consumption and assimilation and assimilation efficiency was measured for six lemmings during a five day period. Food consumption of brown lemmings during summer averaged 0.0273 $\pm$ 0.0045 g wet weight or

Figure 5. Average daily metabolic rate, standard deviation (triangles) and range (bars) of brown lemmings determined by oxygen consumption during four seasons. Numbers indicate sample size.

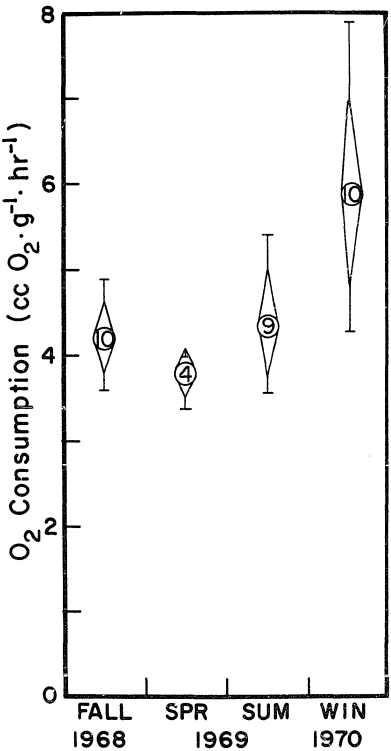


TABLE 2. Average daily metabolic rate (ADMR) of brown lemmings wild caught during spring, summer and fall, and acclimated to -15°C during winter.

Season	n	Animal-day	Average body weight (g) ± 1 S.D.	ADMR (cc/g•hr) ± 1 S.D.	Significance Range[1]
Fall 1968	8	14	56.7 ± 10.0	4.24 ± 0.41	
Winter 1969	10	18	62.7 ± 15.5	5.90 ± 1.06	
Spring 1969	4	8	75.5 ± 18.3	3.79 ± 0.28	
Summer 1969	8	14	55.3 ± 16.7	4.46 ± 0.56	

[1]Solid line in each verticle plane indicates no significant difference between sample means as measured by Duncan's New Multiple Range Test, incorporating Kramer's modification for unequal sample size.

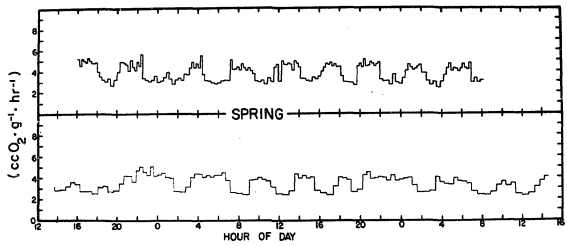


Figure 7. ADMR of two representative brown lemmings captured during summer. Temperature was 10°C and photoperiod (L:D) was 24:0.

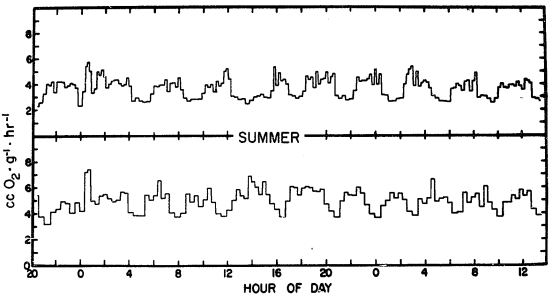


Figure 8. ADMR of two representative brown lemmings captured during summer and acclimated to and tested at 5°C and a photoperiod (L:D) of 12:12. Temperature and light conditions approximate those to which lemmings are exposed at Barrow during fall.

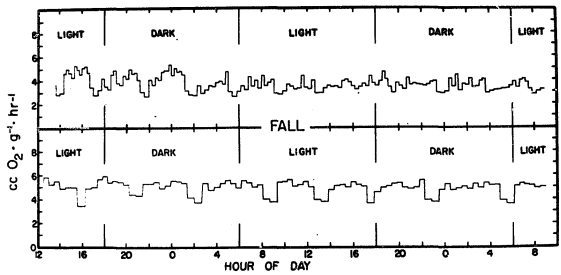


Figure 9. ADMR of two representative brown lemmings captured during summer and acclimated to and tested at -15°C and a photoperiod (L:D) of 3:21. Temperature and light conditions approximate those to which lemmings are exposed at Barrow during winter.

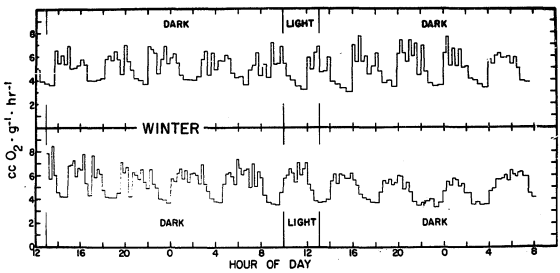


Figure 10. Average period, ± standard deviation (triangles) and range (bars) of the short endogenous cycle of oxygen consumption of brown lemmings during four seasons. Numbers indicate sample size.

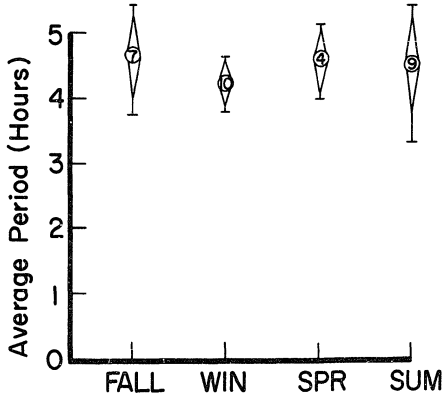
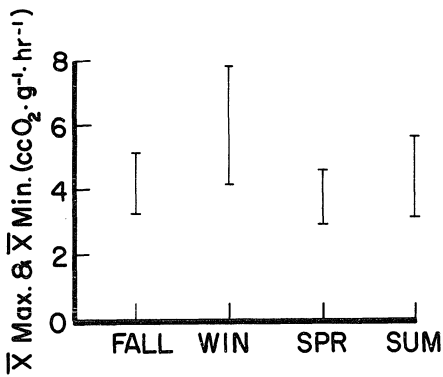


Figure 11. Average maximum and average minimum oxygen consumption in short endogenous cycles of brown lemmings during four seasons.



0.0191 ± 0.0032 g dry weight per g of animal/hr. Considering that the body weight of animals averaged 42.2 g, this amounts to 27.6 g wet weight of food and 19.3 g dry food, or 65% and 46% of the body weight per day. Assimilated energy averaged 27.8 ± 7.0 $cal \cdot g^{-1} \cdot hr^{-1}$ or 28.2 $kcal \cdot animal^{-1} \cdot day^{-1}$ and average assimilation efficiency was 31.1 ± 4.1%.

Activity

Average activity index of brown lemmings was highest in spring and lowest in summer, although differences were not significant (Fig. 12, Table 3). No circadian rhythm in activity was measured during any season, as shown by measurements from representative animals from each season (Fig. 13-16), and no difference in activity index measured during light and dark hours was noted (Table 3). A short cycle in activity, similar to that found in ADMR, was noted for all animals during each season. Average period of the cycle ranged from 4.2 hours in fall to 4.8 hours during summer, and averaged 4.4 hours for all seasons (Fig. 17). However, the average cycle length was not significantly different among seasons.

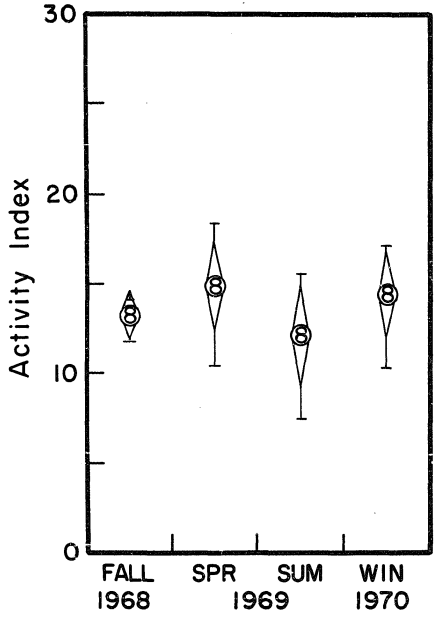


TABLE 3. Average hourly activity index of brown lemmings wild caught during spring, summer and fall, and acclimated to -15°C during winter.

Season	n	Animal days	Average body weight (g) ± 1 S.D.	Average total hourly activity index ± 1 S.D.	Significance Range[1]
Fall	8	21	54.9 ± 11.9	13.3 ± 2.7	
Winter	8	23	63.7 ± 16.2	14.6 ± 3.1	
Spring	8	21	60.0 ± 12.5	15.0 ± 4.9	
Summer	8	16	58.7 ± 12.2	12.2 ± 4.7	

Season	Light:Dark (hrs)	Average hourly activity index in light ± 1 S.D.	Average hourly activity index in dark ± 1 S.D.	P
Fall	12:12	13.2 ± 2.7	13.4 ± 2.8	>0.60
Winter	3:21	13.9 ± 1.6	14.5 ± 3.3	>0.60
Spring	24:0	15.0 ± 4.9	---	
Summer	24:0	12.2 ± 4.7	---	

[1] Solid line in each verticle plane indicates no significant difference between sample means as measured by Duncan's New Multiple Range Test, incorporating Kramer's modification for unequal sample size.

Figure 13. Locomotor activity of two representative brown lemmings captured during spring. Activity index is the number of two minute intervals per hour in which activity occurred. Temperature was 15°C and photoperiod (L:D) was 24:0.

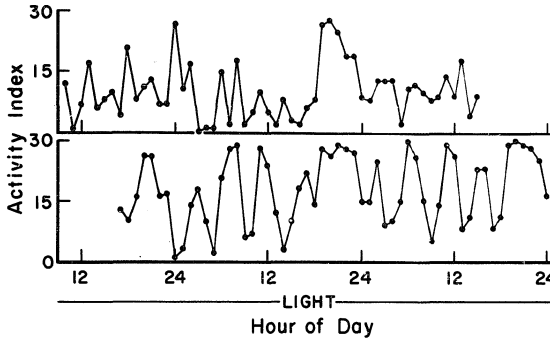


Figure 14. Locomotor activity of two representative brown lemmings captured during summer. Activity index is the number of two minute intervals per hour in which activity occurred. Temperature was 10°C and photoperiod (L:D) was 24:0.

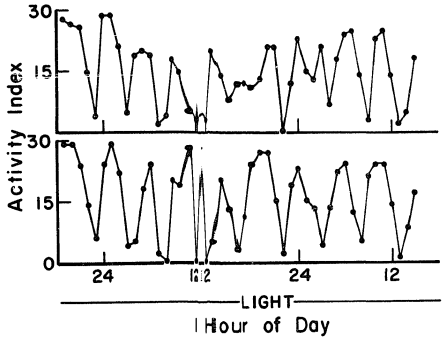


Figure 15. Locomotor activity of two representative brown lemmings captured during fall. Activity index is the number of two minute intervals per hour in which activity occurred. Temperature was 5°C and photoperiod (L:D) was 12:12.

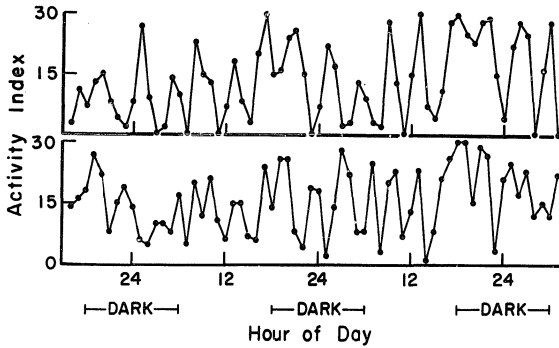


Figure 16. Locomotor activity of two representative brown lemmings captured during summer and acclimated to and tested at -15°C and a photoperiod (L:D) of 3:21. Temperature and light conditions approximate those to which lemmings are exposed at Barrow during winter. Activity index is the number of two minute intervals per hour in which activity occurred.

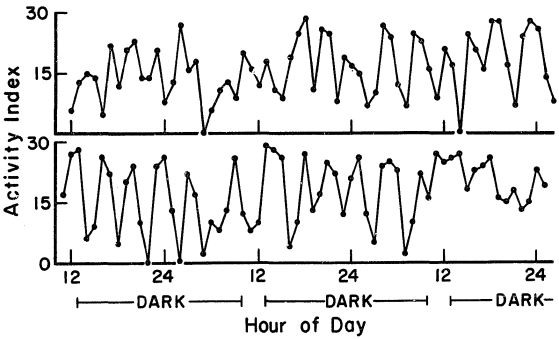
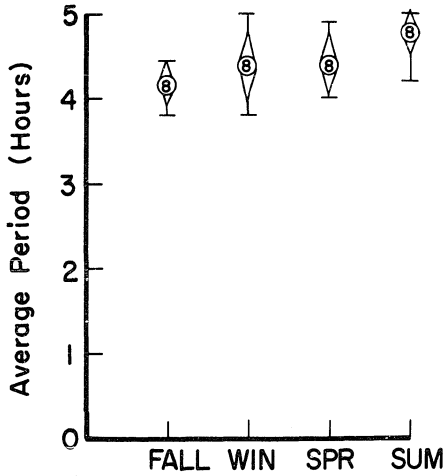


Figure 17. Average period, ± standard deviation (triangles) and range (bars) of the short endogenous cycle of locomotor activity of brown lemmings during four seasons. Numbers indicate sample size.



DISCUSSION

Oxygen Consumption

Three different measurements of respiratory rate have been frequently used in small mammal energetics. Basal metabolic rate (M_b) is a measure of caloric requirements for minimum physiological functions. It is determined by measuring resting, postabsorptive animals at an ambient temperature within their thermal neutral zone. Since ideally M_b excludes metabolism due to activity, thermoregulation and digestion, it is a useful comparative measure of the biological intensity of an organism (Morrison 1948). Resting metabolic rate (M_{rest}) is the metabolic requirements of a fed animal at rest, measured at any ambient temperature. It has been most widely used to measure the metabolic rate of animals at different ambient temperatures. Both M_b and M_{rest} of brown lemmings have been reported by Coady (MS). Average daily metabolic rate is the average metabolic rate of animals measured over a long period of time. Food and water are provided and the test chamber is large enough to permit activity during measurement. Average daily metabolic rate is more useful than M_b and M_{rest} measurements for ecological studies. In addition to permiting "normal" activity and feeding patterns, ADMR is usually measured at temperature and light conditions similar to that found in the animal's natural habitat. Therefore, metabolic requirements which approximate those of free ranging animals are best obtained using ADMR measurements.

Average daily metabolic rate of brown lemmings was greater than either M_b or M_{rest} (Coady, MS) measured during the same season (Table 4).

TABLE 4. Basal (M_b), resting (M_{rest}) and average daily metabolic rate (ADMR) of brown lemmings measured during the same season.

Season	Temp °C	M_b($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)[1]	M_{rest}($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)[1]	ADMR($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)[2]
Spring	5	1.78	2.36	3.79
Summer	10	1.77	2.11	4.46
Fall	5	1.83	3.19	4.24
Winter	-15	2.18	4.15	5.90

[1]From Coady (MS).

[2]From Table 2.

Average daily metabolic rate exceeded M_{rest} by 33% in fall and 111% in summer. Grodzinski (1966) found an increase in ADMR over M_{rest} of 20 and 25% for Clethrionomys rutilus and Microtus oeconomus, respectively, measured at 20°C during summer. The greater increase in ADMR over M_{rest} of brown lemmings during summer may be due to reduced energy requirements for thermoregulation, resulting in a relatively low M_{rest} (Table 4). Other authors have found M_{rest} to be greater than ADMR during similar seasons. Grodzinski and Gorecki (1967) reviewed several studies of Apodemus flavicollis, A. agrarius, Clethrionomus glareolus and Microtus arvalis in which M_{rest} was 18-32% greater than ADMR during the same season. Similarly, Hansson and Grodzinski (1970) found that M_{rest} of Microtus agrestis at 20°C was 33% greater than ADMR. "Stress" and restricted movement were suggested as causes of unusually high M_{rest}, while low ADMR's probably result from averaging periods of voluntary activity and rest during long ADMR tests (Grodzinski and Gorecki 1967).

Seasonal ADMR's of brown lemmings fall within the range of values measured for other small mammals (Table 5). The similarity in ADMR of lemmings during spring, summer and fall (Table 2) is probably due to similar energy requirements for thermoregulation and locomotor activity during each season. The significantly higher ADMR of lemmings during winter (Table 2) may result from the added energy requirement for thermoregulation at a cold temperature. Other studies in which ADMR of small mammals has been measured seasonally have found a lower oxygen consumption during winter than during summer (Table 5). However, in those studies ambient temperature during tests was the same during all

TABLE 5. Average daily metabolic rate (ADMR) of several small mammals reported in the literature.

Species	$\bar{x}$ body wt (g)	Season	Temp (°C)	ADMR ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	Reference
Microtus agrestis	13-29	Lab	20°	3.95	Hansson and Grodzinski 1970
Microtus oeconomus	26	Summer	20°	4.62	Grodzinski 1966
Microtus oeconomus	37	Spring	20°	3.31	Gebczynska 1970
	22	Summer	20°	4.49	
	26	Fall	20°	4.31	
	21	Winter	20°	3.65	
M. oeconomus	28	Lab	10°	5.00	Grodzinski 1971
	26	Lab	15°	4.62	
M. oeconomus	25-35	Lab	20-30°	4.00	Wiegert 1961
Clethrionomys rutilus	25	Summer	20°	4.24	Grodzinski 1966
C. rutilus	24	Lab	10°	4.87	Grodzinski 1971
	25	Lab	15°	4.24	
	24	Spring	20°	4.07	
C. glareolus	24	Summer	20°	4.29	Gorecki 1968
	19	Fall	20°	3.79	
	20	Winter	20°	3.65	
C. gapperi	19	Lab	13°	6.33	Buckner and Bergeron 1973
	19	Lab	17°	5.92	
	20	Lab	21°	4.59	

TABLE 5. Continued.

Species	$\bar{x}$ body wt (g)	Season	Temp (°C)	ADMR ($cc O_2 \cdot g^{-1} \cdot hr^{-1}$)	Reference
Dicrostonyx groenlandicus	55-84	Lab	20°	3.94	Fisher and Needler 1957
	55-84	Lab	25°	4.21	
	55-100	Lab	30	3.53	
Microtus oeconomus	33.9	Spring	15	4.28	Whitney 1973
	29.3	Summer	15	4.36	
	19.9	Fall	8	5.46	
	16.7	Winter	-3	7.26	
Clethrionomys rutilus	20.3	Spring	15	5.08	Whitney 1973
	24.3	Summer	15	4.61	
	16.8	Fall	8	4.90	
	15.8	Winter	-6	6.79	

seasons, and therefore seasonal differences in oxygen consumption were probably due to differences in activity or physiological requirements other than thermoregulation.

Average oxygen consumption in dark and light was not significantly different ($P<.001$) in lemmings tested during fall and winter. During spring and summer when the photoperiod consisted of 24 hours of light no diel cycle in oxygen consumption of lemmings was apparent (Fig. 8 and 9). Wiegert (1961) found a bimodal pattern of 24 hour oxygen consumption in recently captured Microtus pennsylvanicus, while no well defined biomodality was seen in animals held in captivity several days before testing. Since brown lemmings in this study were held in captivity for one or more weeks before testing, any diel pattern in oxygen consumption could have disappeared before the animals were tested. However, captive animals were maintained at temperature and light conditions approximating those in their natural habitat to minimize changes in behavioral and physiological activities. Wiegert (1961) does not state the temperature and light regime under which his test animals were held.

A 24 hour pattern of oxygen consumption has been reported by several workers. Hansson and Grodzinski (1970) found an increase in 24 hour metabolic rate of Microtus agrestis from Sweden beginning just before dark and lasting during late afternoon and evening. Hart (1950, 1952) found oxygen consumption of white mice to be greatest during night. Grodzinski (1971) found a daily rhythm in oxygen consumption of Microtus oeconomus and Clethrionomys rutilus during summer in interior Alaska. Both species

of voles showed a slight nocturnal peak which increased at lower ambient temperatures, although long periods of increased oxygen consumption were not related to hours of darkness. Fisher and Needler (1957), however, found no diel cycle in oxygen consumption of the varying lemming exposed to the light cycle at the latitude of Toronto, Canada.

While no indication of 24 hour cycles in metabolic rate were observed, short cycles or "short endogenous rhythms" referred to by Folk (1966) were obvious in all animals. The cycles were not syncronized among individuals nor was the frequency or amplitude of the cycles influenced by time of day or light-dark changes. The short cycle of oxygen consumption in brown lemmings continues under constant environmental conditions and is independent of light changes. It is therefore persistent or endogenous (Ashoff 1960).

The short cycle has been related to feeding activity (Fearson 1947). At cold temperatures feeding periods may be more frequent or longer in duration to compensate for increased metabolic rate. Therefore, if the short term cycle were related to increased muscular or physiological activity associated with feeding, the frequency of cycles or the duration of increased metabolic rate of each cycle would increase during the winter. However, an increase in the duration of high oxygen consumption during winter over that in other seasons did not occur (Fig. 6-9). While the period of the short cycle was shortest during winter, the differences were not significant (Fig. 10). Therefore, short endogenous rhythms in brown lemmings are probably due to factors other than those associated with feeding. Similarly, Fisher and Needler (1957) found no difference

in cycle duration of varying lemmings within a temperature range of 20 to 30°C.

Other factors influencing the period of short cycles may be size or age of the animals. Crowcroft (1954) suggested that the period decreases with size of the animal, which is presumably related to weight specific metabolic rate. However, short cycle periods in oxygen consumption of various rodents reported by Morrison (1948) do not support Crowcroft's hypothesis. Pittendrigh and Daan (1974) reported that the period of free-running circadian activities in gold hamsters, Mesocricetus auratus, and two species of deer mice, Peromyscus maniculatus and P. leucopus, decreases with age. While brown lemmings measured during winter had been held in captivity longer than animals measured during other seasons and therefore may have been the oldest test group, the period of the short cycle was not significantly shorter than that at other seasons (Fig. 10). Further data are needed before this hypothesis can be tested with brown lemmings.

Food Consumption

Food habits of brown lemmings near Barrow have been generally described by Thompson (1951, 1955b, 1955c), Pitelka (1957) and more recently in detail by Batzli et al. (1975). During summer, brown lemmings prefer moist habitats where monocots form the major forage. Batzli et al. (1975) found that monocots account for 70 to over 90% of the diet during summer. During winter when monocots are less available, they account for approximately 55% of the diet, while mosses account for most of the remainder.

Food consumed by lemmings must supply the energy required for maintenance, growth and reproduction. Gross caloric intake is the energy content of ingested food, while net caloric intake or assimilated energy is calculated by subtracting the calories lost in feces and urine from gross caloric intake. Net caloric intake represents the energy available for body maintenance and production. Net caloric intake divided by gross caloric intake is a measure of assimilation efficiency.

The total dry weight of forage ingested daily represented about 46% of the animal's body weight, similar to that measured for lemmings in other studies. Batzli et al. (1975) measured an intake by juvenile lemmings of two species of grass which ranged from 41 to 61% of the animal's body weight/day. Food consumption by adult lemmings averaged 32% of their body weight/day. Schultz (1964) found that adult lemmings consumed approximately 32% of their body weight in dry monocots.

Net caloric intake of forage should be similar to energy requirements determined by ADMR tests. Net caloric intake averaged 27.8 $cal \cdot g^{-1} \cdot hr^{-1}$ (assuming a caloric equivalent of 4.8 $cal \cdot cc O_2$). Therefore, energy requirements of brown lemmings during summer were 23% greater when determined by food consumption than by oxygen consumption. However, net caloric intake of forage was determined using lemmings captured during summer 1968, while summer ADMR was determined using animals captured during summer 1969. Resting metabolic rates measured at 10°C of lemmings captured during both summers were 29% higher in 1968 than in 1969 (Coady, MS). This difference in M_{rest} was attributed primarily to differences in fur insulation (Coady, MS). The same effect probably

caused the difference in summer energy requirements determined by food and by oxygen consumption in this study.

Assimilation efficiency of brown lemmings eating monocots is low. The 31.1% efficiency determined in this study is similar to that found for brown lemmings by other workers. Batzli et al. (1975) obtained an assimilation efficiency of 35% for brown lemmings eating monocots, and Batzli et al. (1975) reported an efficiency of 36% for lemmings eating the sedge, Eriophorum angustifolium. Assimilation efficiencies of small mammals from non arctic areas are considerably greater than those for brown lemmings. Drozdz (1971) reported a digestibility of 55% for grass eaten by Arvicola terrestris and Batzli et al. (1975) found a digestibility of 56% for grass eaten by Microtus californicus. Gebczynska (1970) found an assimilation efficiency of 69% during summer and 74% during fall by Microtus oeconomus eating green grass and herbs. High efficiency values have been reported by McManus (1974) for Clethrionomys gapperi eating pelleted rations.

Low digestibility of food contributes to the high rate of food consumption by lemmings as compared with other microtines. Gross caloric intake of brown lemmings reported by Batzli et al. (1975) average 60 kcal/day for 40 g animals, while a consumption rate of approximately 90 kcal/day was found for 42 g brown lemmings in this study. The above values of gross and net caloric intake are probably minimal estimates of summer energy requirements, since they do not include requirements for growth, reproduction and thermoregulation at colder temperatures. Increased activity of free ranging lemmings associated with foraging would probably further increase energy

requirements over the above measurements.

Activity

Seasonal rhythms are apparent in almost all animals (Cloudsly-Thompson 1961), and brown lemmings are no exception to this rule. Seasonal changes in reproductive intensity (Mullen 1968), body size (Krebs 1964), fat content (Coady, unpubl.) and tissue fatty acids (West and Coady 1974) have been reported. McNab (1963) and West (1968) have demonstrated a decrease in physical and physiological functions for activities other than thermoregulation during winter in Peromyscus spp. and ptarmigan, Lagopus lagopus, respectively. Stebbins (1971, 1972) and Martin (1973) have reported a decrease in locomotor activity during winter in several species of Peromyscus, Clethrionomys gapperi and C. rutilus. Therefore, except for thermoregulation, activities such as movement, reproduction and growth in these species are minimized during periods of cold stress.

The similarity in level of seasonal activity of brown lemmings in this study suggests the need for this species to remain active throughout the year. Lemmings do not undergo torpor during winter, as do deer mice, P. maniculatus reported by Stebbins (1971), nor do they store food to minimize foraging activity during winter, as do many species of small mammals. Foraging activity of brown lemmings during winter is probably greater than during summer because of increased difficulties in obtaining food and because of increased energy requirements for thermoregulation (Coady, MS). Therefore, even captive lemmings supplied with food ad

libitum apparently retain the activity pattern of wild animals in the cold.

The circadian rhythm is the most common biological rhythm (Cloudsly-Thompson 1961; Folk 1966), and has been reported for many species of mammals, including numerous rodents. The absence of a circadian rhythm in locomotor activity of brown lemmings in this study may have been due to isolation from the natural environment by captivity for a period of time before testing (see above). However, mammalian circadian rhythms are usually very persistent (Cloudsly-Thompson 1961) often being altered greatly in phase, but very little in period length. Therefore it is unlikely that a detectable circadian rhythm existed in wild lemmings and disappeared shortly after capture. Nevertheless, Swade and Pittendrigh (1967) reported circadian locomotor rhythms in three brown lemmings from arctic Alaska which were nocturnal in spring but became diurnal in summer. Conversely, Melchior (pers. comm.) noted that brown lemmings were most active during "night" hours in June, July and August. While live trapping lemmings near Barrow, Alaska, he reported that 60% of the animals were captured between 8 pm and 8 am. Observations of lemmings in an enclosure also suggested a nocturnal activity pattern. However, Hansen (1957) found no circadian rhythm in varying lemmings born and raised in captivity.

Folk (1966) noted that insectivores and some rodents are characterized by a short endogenous activity rhythm of two and one-half to eight hours which is not influenced by photoperiod. A short rhythm was the only activity rhythm found in brown lemmings in this study. The short cycle was, as noted by Folk (1966), uniform and persistent under different

photoperiods. Pearson (1962) reported a three hour short cycle in C. rufocanus and C. glareolus, and noted that it was the basic rhythm for C. rufocanus. While the short cycle may also be the primary rhythm for C. glareolus, the cycle in this species could be altered by photoperiod changes. Short cycles in activity of small mammals have been reported by many workers, including Stebbins (1972), Crowcroft (1954), Miller (1955) and others.

Daily pattern of oxygen consumption reflects locomotor rhythms in several mammals (Hart 1950, 1952; Hansson and Grodzinski 1970; Ashoff and Pohl 1970; Grodzinski 1971). This appears to be true for brown lemmings as well. Neither ADMR nor locomotor activity measurements indicated a circadian rhythm. However, both measurements reflected a well defined short cycle. Average period of the ADMR and locomotor activity short cycle were similar during each season, and small differences which do exist are probably due largely to difficulties in determining the precise length of cycles.

SUMMARY

Bioenergetic data involving the brown lemming are limited. The purpose of this study was to provide information on energy relationships involving this important herbivore, and thereby contribute to an understanding of ecological relationships in arctic ecosystems.

Average daily metabolic rates measured at temperature and light conditions approximating those to which lemmings are exposed at Barrow probably provide a reasonable approximation of seasonal energy requirements of free ranging animals. Energy requirements of lemmings measured during spring, summer and fall were not significantly different, and ranged from 3.79 to 4.46 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$. Significantly higher ADMR's of 5.90 $cc O_2 \cdot g^{-1} \cdot hr^{-1}$ in lemmings acclimated to -15°C during winter were recorded. Greater energy requirements during winter were probably due to increased requirements for thermoregulation, since average activity indices were similar during all seasons. Average daily metabolic rates were somewhat greater than M_{rest} measured at corresponding temperatures and seasons (Coady, MS) due to energy requirements for locomotor activity. Energy requirements of free ranging lemmings may be greater at certain times than ADMR reported here because of increased energy requirements for foraging and intraspecific interaction. Energy requirements for reproduction and growth were not measured. While no circadian rhythm in either oxygen consumption or locomotor activity was detected, a short endogenous rhythm of four to five hours in both observations was recorded for all individuals tested. This suggests that short cycles in oxygen consumption of lemmings may be

due primarily to locomotor activity. The cause of these short activity cycles are unclear, although they are probably not directly related to feeding.

Food consumption was high and efficiency of assimilation was low during the summer season in which feeding trials were conducted. Dry weight of natural forage consumed averaged 46% of the lemming's body weight per day, while efficiency of assimilation averaged 31.1%. Assimilation efficiency of natural food by lemmings is considerably lower than values reported for microtine rodents at more southern latitudes, and suggests that a large amount of time and energy must be devoted to foraging activities.

Metabolic rate determined by food consumption in summer 1968 was 23% greater than that determined by oxygen consumption during the same season in 1969. This difference is similar to that measured in M_{rest} tests at 10°C in summer 1968 and 1969 (Coady, MS), and suggests that annual differences in energy requirements for free ranging lemmings did exist between those two years.

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CONCLUSION

Metabolic rates of brown lemmings increased with decreasing ambient temperatures following the Newtonian model (Law of Cooling), as do most homeotherms. However, thermal conductance was considerably below that predicted on the basis of body size, apparently because of enhanced fur insulation. Conductance of lemmings was greater during three seasons in 1968 than during the same seasons in 1969. This was attributed to colder subnivian temperatures during the winter of 1968-69 which intensified fur insulation and decreased conductance. Greater precipitation and cooler temperatures during the snow free period in 1969 may have helped maintain low conductance in lemmings during that period. However, the similarity in conductance of lemmings captured during spring and summer 1969 and in animals acclimated to 5°C and -15°C is probably due to consistently cool and relatively small changes in ambient temperatures.

Low M_{max} of lemmings during seasons in 1968 compared to the same seasons in 1969 are also attributed to differences in cold exposure during the preceding winters. Colder subnivian temperatures during winter 1968-69 *vs.* 1967-68 may have resulted in greater cold exposure and improved metabolic capability during the following seasons. Uniformity in M_{max} of lemmings captured during spring and summer 1969 and animals acclimated to 5°C and to -15°C may also have been due to cool and relatively constant temperatures to which lemmings were exposed.

Reasons for a gradual decrease in conductance and increase in

M_{max} during consecutive seasons in 1968 are unclear, and further studies to document the extent to which seasonal and annual differences in temperature influence these metabolic parameters are certainly needed. The absence of distinct seasonal changes in M_{rest} and M_{max} of lemmings in this study needs further investigation. Similar observations are unusual in the literature, although metabolic parameters of seasonally acclimatized arctic species have received little attention.

While the regression coefficient of M_b on body weight is similar to that predicted by standard equations, M_b ranged from 32 to 80% above standard rates. High M_b supports the hypothesis that M_b may be phylogenetically adaptive, and that Microtines, having originated in northern latitudes, have higher M_b than expected on the basis of body size. Factors responsible for higher M_b during 1968 than during 1969 are unknown.

Average daily metabolic rates of lemmings were significantly higher during winter than during other seasons, primarily because of increased requirements for thermoregulation. Locomotor activity of lemmings was not significantly different during four seasons. No circadian rhythm in ADMR or activity measurements was detected, although a distinct short endogenous cycle in both oxygen consumption and locomotor activity was noted in all animals. Changes in season or photoperiod did not influence the pattern of activity or oxygen consumption of lemmings in this study, and factors influencing the length or amplitude of the short cycle are uncertain.

Consumption of natural food during summer was high and rate of

assimilation was low, resulting in a low efficiency of assimilation. Because lemmings are exposed to temperatures below thermal neutrality throughout most of the year, and because efficiency of assimilation is low, large quantities of food must be ingested to provide energy for maintainence, growth and reproduction. Additional studies are needed to determine energy budgets of free ranging lemmings. Energy requirements for production, such as growth, pregnancy and lactation need to be determined.

In order to better understand the influence of weather on metabolic parameters of brown lemmings, microenvironmental conditions in lemming habitat need to be more thoroughly measured. Knowledge of lemming subnivian habitat, which persists for approximately nine months per year, is particularly deficient. Future studies must place greater emphasis on ecological relationships existing during the long winter season.

The influence of factors other than weather on metabolic relationships also need study. For example, energy requirements of lemmings may be influenced by population density. Changes in M_{rest}, M_b and M_{max} may reflect the "quality" of animals during the cycle of abundance, while ADMR may be altered by changes in intra- and interspecific relationships during the population cycle.